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The Formal Model for *Coccinella septempunctata* for implementation in Animal Landscape and Man Simulation System

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Abstract

We present the Formal Model for the seven-spotted ladybird *Coccinella septempunctata* L., to be implemented in the Animal Landscape and Man Simulation System. This agent-based model is designed to dynamically interact with pre-existing aphid species models, providing a foundation for studying the effects of landscape-scale management on these species. It also serves as a crucial component in developing a model system to support the analysis of Integrated Pest Management strategies. We present an extensive literature survey of *C. septempunctata* ecology and behaviour. The model primarily considers temperature and aphid prey availability as the major driving factors, given the species' reliance on aphids during its juvenile stage. Mechanisms and parameters are, as far as possible, derived from previous models and literature studies. Each major section of behaviour is described first in terms of what is known ecologically and secondly in terms of planned implementation. We present a description of the factors included in the model and those consciously excluded, providing justifications for these decisions. Additionally, we discuss aspects of the model's implementation and identify data gaps, highlighting specific areas for future improvement. The next phase involves the implementation and calibration of the model.

Key words: Agent-based model, ALMaSS, ecology and behaviour, landscape model, seven-spotted ladybird

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Introduction

Coccinellidae are key predators of pests, including aphids, mealybugs, mites and whiteflies (Obrycki and Kring 1998). The ladybird beetle, *Coccinella septempunctata* L. (Family: Coccinnellidae, Order: Coleoptera), is a widely recognised entomophagous predator feeding on soft-bodied insect pests. Although it is not the only important or abundant species of coccinellid for pest control (Magagnoli et al. 2024), it is probably the European species that is best studied, and as such was chosen as the first ladybird to be modelled in this study.

The adult and larval stages of *C. septempunctata* primarily feed on a wide range of aphid species, thereby playing an important role in the biological control of these

pests worldwide. Although native to Europe, Asia and Northern Africa, *C. septempunctata* has established itself in North America, where it was introduced in 1956 as a biological agent to mitigate aphid infestations in agricultural crops (Angalet et al. 1979). The use of coccinellids for the biological control of aphid populations has been a common practice for decades. Over its lifespan, a seven-spot ladybird can eat a mean of 3365.5 cotton aphids (El-Sayad et al. 2024) and exhibits a type II functional response in the laboratory and field (Hamid et al. 2020; Yang et al. 2022; Wu et al. 2023). However, literature studies underscore the nuanced effectiveness of biological control strategies, highlighting that the impact of coccinellids on aphid suppression can vary significantly across different contexts.

Kindlmann and Dixon (1999) developed a hypothesis to explain the underlying problem with aphid control by ladybirds. Their generation time ratio (GTR) hypothesis considered that the efficiency of predators as biological control agents is negatively correlated with their generation time relative to their prey. This effect occurs because when predator generation time is extended, the depletion effect on a prey patch population is reduced as the prey continues to reproduce. Indeed, depletion of the prey source is not in the interest of the predator, given, in this case, the low mobility of the larvae. However, aphid control can be achieved when multiple control agents are active; for example, complementary control can occur with a parasitoid (Snyder et al. 2004).

Despite these problems, there have been many attempts to model the ladybird-aphid interactions for system understanding and biological control, but this has not been without difficulty. The inability of models to accurately predict aphid population dynamics for practical applications arises from the highly variable fluctuations in aphid numbers, driven by both intrinsic factors (such as size, fecundity, mortality, and migration rates) and external factors, particularly weather conditions, with temperature being a key influence. Consequently, these models are often not sufficiently robust for reliable forecasting, as their predictions are contingent on unpredictable seasonal weather patterns (Kindlmann and Dixon 2010).

There are, therefore, three confounded problems in modelling ladybird-aphid interactions. Although *C. septempunctata* can feed on various types of food, it cannot develop or reproduce on non-aphid food (Majerus 1994); hence, the key problem is predicting the occurrence of the aphids. There is also the need to develop a multiple-species system to predict control. The third problem is that the occurrence of ladybirds (and other species) is not only determined by the presence of aphids but also by a wide range of other environmental and ecological factors. These factors include land-use changes, agricultural management, climate, and interactions with ladybird predators and diseases.

In this formal model (Topping et al. 2022), we address these problems initially from the ladybird perspective by splitting the issue into these three problems but assuming that the occurrence of aphids in time and space is predictable. Our model will be implemented in the Animal Landscape and Man Simulation System (ALMaSS; Topping et al. 2003; Topping 2022), designed as a C++ system of spatially explicit agent-based models for use in predicting the effects of human landscape management on a range of key animal species. Concurrently with the development of this model, a spatially and temporally detailed model of aphids that utilises up-to-date geographical data and considers realistic farming practices is under development in ALMaSS (Thomsen et al. 2024). This leaves the problems of modelling the ladybird population and spatial dynamics, and context

specificity. Once achieved, by combining the two models (aphids and ladybirds), we aim to provide a tool for understanding both the best control aspects and a deeper understanding of the population dynamics of the ladybird itself.

Modelling ladybird ecology and behaviour

Several predator-prey population dynamics models have been proposed to investigate different aspects of interactions between aphids and ladybirds at different scales. For example, mathematical models investigating the within-season population dynamics in an ecological patch (e.g. Kindlmann and Dixon 2003; Xia et al. 2018; Gabbriellini 2019). These models do not consider between-patch movement, but this is the focus of another model that implements very simple interactions describing movement between yucca plants and relates feeding activities to plant attraction (Brown et al. 2020). Models can, however, include extensive biological information like the model of *C. septempunctata* and *Aphis gossypii* by Xia et al. (2018). This model includes interactions between all the ladybird life stages which are affected by both temperature and host growth. The model also includes the effect of plant leaf-area on aphid carrying capacity and ladybird search efficiency. Given the detailed data on which these models are based, they provide an excellent basis for developing the ALMaSS ladybird model and are used extensively below.

Modelling ladybirds spatially

These simpler mathematical ladybird-aphid models were further extended to landscape-scale models which include redistribution of aphids and ladybirds among a larger number of patches at the end/beginning of each season. For example, in the model by Houdková and Kindlmann (2006) (being an extension of Kindlmann and Dixon (2003)), aphids were mixed and redistributed at random to the patches while ladybirds were redistributed according to the optimal oviposition rules. Although this model clearly shows the importance of scale in considering the dynamics of ladybird-aphid systems, it includes little spatial realism, and does not include the habitat quality of individual habitat patches.

Bianchi and Van Der Werf (2003, 2004) and Bianchi et al. (2007) developed a spatially explicit model of the population dynamics and foraging performance of *C. septempunctata* in simplified landscapes. Their model, developed in the GIS software package PCRaster, used 20 × 20 m spatial resolution and 1-hour time-steps to simulate the rapid dispersal dynamics of the ladybirds. Although the realism has been greatly enhanced, their calculations are performed for each cell as a sub-population. The landscape elements can hold some parameters important for ladybirds, such as the carrying capacity for aphids, which changes during the season, but only broad categories of landscape elements are considered.

Here, we build on many of Bianchi et al's (loc cit) ideas but include two key areas of increased realism. First, the ladybird model will be integrated into a highly detailed, dynamic landscape simulation in ALMaSS (Topping et al. 2003; Topping and Duan 2024b, a). Furthermore, the model described here is an agent-based model representing each individual and its behaviour as a unique entity. This approach allows the inclusion of greater descriptive power in this model compared to the other models described here, although at the cost of a higher demand for computational resources.

Aim and purpose

The model aims to create a realistic representation of ladybirds moving through landscapes in space and time and to generate emergent population dynamics from the sum of the behaviours of the individual ladybird agents. This means we want to include the interactions between individual ladybirds and their local environment, such as prey density and management. Since these factors co-vary and interact, a broader system-based perspective is needed to unravel this complexity and determine the relative importance of each of the factors. The ALMaSS modelling approach, coupling a detailed spatio-temporal landscape model with agent-based population modelling, has been shown to be a useful tool for understanding the functioning of populations under multiple stressors at larger spatial and temporal scales (Topping et al. 2016; Topping and Luttik 2017; Ziółkowska et al. 2021). Therefore, using the ALMaSS framework and ladybird model, we want to generate emergent population properties driven by farm management changes and weather and use this to predict the predation pressure on aphids. Later, the aim is to integrate this model with a detailed model for aphid populations modelled in the same landscapes within the ALMaSS framework. In its final form, the ladybird model should be utilised as a component of a simulation-based index for measuring management impacts on beneficial arthropods in northern and central European agricultural landscapes, and provide a critical component in developing a model system to support analysis of Integrated Pest Management (IPM) strategies.

This model heavily relies on, but also informs, the aphid species model (Thomsen et al. 2024). Since the ladybird is a highly specialised aphidophagous predator, a lot of its decision-making (e.g., direction of migration, time of hibernation) is directly or indirectly influenced by the availability of aphids. On the other hand, by reducing the aphid population, the ladybirds can initiate an elaborate pattern of local or global decline in aphid numbers. This dynamic can, in turn, trigger another link of interdependence when a significant fall in the local aphid population causes cannibalism among the ladybirds. The model is designed to be run along a set of different aphid species, thus creating a stack of species of prey and predators interacting within the same landscape.

Theoretical framework

In this model, we will use an agent-based modelling approach (Grimm and Railsback 2005). In agreement with this approach, each individual ladybird beetle will be represented by a separate code object with defined properties (such as age, appetite, or the number of ovarioles developed). Each object in our model can be in one and only one state. Individuals will switch between different states during their lifetime, defining their physiological or developmental status.

In this model, in addition to biological age and time spent in the current morph, the total number of eggs to be produced is assumed to be an essential characteristic of the individual. Exposure to specific weather and prey conditions can influence the total number of eggs produced prior to maturity. Once oviposition has begun, the total number of eggs is a proxy for life expectancy. Once an individual has laid all its eggs, it dies, having fulfilled its reproductive purpose.

Our spatially explicit model uses the ALMaSS to provide a highly detailed (1 m^2 spatial resolution), dynamic landscape representation. Our model agents will navigate through this landscape, read its properties (such as vegetation type and presence of resources) and use the information gained to manifest different behaviours. For example, ladybirds tend to move to vegetation with a higher potential to be infested by aphids in June but move towards the woodland for hibernation in August-September. In ALMaSS, the temporal dynamics of the landscape ensure that farming activities (including pesticide spraying that can cause damage to the ladybird population) are performed throughout the year according to crop management plans individually tailored to each crop. In addition, vegetation growth models enable vegetation height and leaf cover to be updated daily. Crop rotations ensure that each farm follows its multi-annual field rotation plan, while the crop distribution in the landscape is based on the local agricultural registry from the European Common Agricultural Policy subsidy claims (Ziółkowska et al. in prep).

The time step of our model is one day, which means that the external factors, like temperature, rainfall, and the local abundance of aphids, are updated daily. At the same time, there is no upper limit on the number of interactions or activities each individual can perform in one time-step.

The life history parameters used for model development are either based on laboratory or field data collected on *C. septempunctata* or, when no data on this particular species is available, the information from the sister species of ladybirds with a similar life history was used. In these cases, the data was 'calibrated' to fit the known data on *C. septempunctata*, e.g., by correcting for size.

Framing the model

General considerations

This model is a model of the seven-spot ladybird. Therefore, despite being built based on the experimental and observational data collected from various species, the ultimate intention is to represent this single species. This means that (at least in the first iterations of the model) we ignore a plethora of intra-guild interactions, including competition, intra-guild predation and the transfer of diseases and parasites. However, the seven-spot ladybird is a species that includes all the basic behaviours characteristic of the Coccinellidae, and most of these mechanisms are planned in this model. Therefore, this formal model could be adapted in the future, using data from different ladybird species (e.g., characteristics for geographical region), and the intra-guild interactions could be modelled using the model mechanisms (such as cannibalism or competition between individuals).

Mortality

This model does not explicitly model the intra-guild predation of the ladybirds or the influence of parasitism on the population dynamics. Instead, we factor the mortalities due to these causes into general mortality during calibration. We, therefore, risk missing a deterministic population dynamics driver when assigning these mortalities to a general stochastic process. However, the extra work and data

needed to model this correctly mean it is currently out of scope. This omission is a clear limitation of the model, which should be addressed in future developments because of its potential to cause complex non-linear dynamics in space and time.

Although included for temperature extremes, other weather extremes are also likely to cause ladybird mortality. This factor is not modelled explicitly, but it could be important under changing climate conditions or at the edge of the species' range.

A further source of mortality that is difficult to include is parasitism of adults. This is a major mortality, and is very variable, but currently most studies are descriptive or focus on local mechanisms, and thus any modelled relationship is necessarily simple, despite the strong likelihood of closely interconnected population dynamics.

Feeding

This model does not provide a full energetic budget for the ladybird individuals. The main reason for that is that even though ladybirds are specialist predators and aphid abundance defines their life cycle, the range of foods that ladybirds can consume throughout a year in the absence of regular prey is broad. This food could be of both animal and plant origin (Ricci et al. 2005; Hodek et al. 2012). Thus, building a realistic energetic budget would demand more detailed knowledge of prey and other food densities than already aimed for here. Such an undertaking goes well above the limits of this study and may not be important since aphids are the only known essential food source (Hodek 1962; Evans et al. 1999; Berkvens et al. 2010), ensuring oviposition and development. We, therefore, provide a connection only between the aphid food intake and ladybird's growth, development and reproduction. While building a complete energetic budget is out of the scope of this model, we do include proxies. For example, the individual's daily aphid-related appetite follows the development stage and the time of the year, and the development stage and the temperature restrict the daily movement range.

The type of aphid food is clearly an important determinant of growth and fecundity (e.g. see Omkar and Srivastava 2003). However, it is impossible to precisely predict the type and density of food available to the individual ladybirds. We have, therefore, used a categorical approach to prey density and provide a scaler for aphid species quality, which can function when coupled with specific aphid prey models. However, there are limits related to the level of detail related to conditions under which prey density is measured. For example, variations due to crop cultivars are not included in ALMaSS, and off-crop vegetation details are limited. Hence, many details about the effect of food quality cannot be reliably included, even if sufficient knowledge were to be available.

This model uses cannibalism as a 'last resort' action when foraging. This choice is based on an accepted hypothesis that the aim of cannibalism and intra-guild predation is to satisfy the nutritional needs of the individual (Lucas 2013). There is uncertainty in how our model accounts for cannibalised prey in terms of aphid appetite satisfaction. The literature review did not reveal a consistent comparison between the nutritional values and those of the ladybirds' pre-imago stages (subject to cannibalism). To overcome this issue, we have suggested using the proxy of the average individual egg/instar weight (Sengonca and Arnold 2003; Honek et al. 2008).

Movement and hibernation

The tendency of ladybird beetles to travel long distances during autumn aggregation and spring dispersal is well documented. According to the literature, the targets of such long-range migrations are outstanding landscape features, such as mountain peaks (Hodek 1993; Ricci et al. 2005). However, our model is built to be used in the context of ALMaSS simulation for the small to medium-sized landscape windows (10 × 10 km^2 to 50 × 50 km^2) in predominantly agricultural locations. This scale means that we cannot model long-distance functions and make a simplifying assumption that all ladybirds will hibernate within the model landscape in suitable habitats. This simplifying assumption allows us to model the population and impacts consistently with the landscape drivers, but also means that we ignore large-scale spatial dynamics, which are likely to be significant in ladybird population survival.

The ladybirds use prominent local landscape features (stones, single trees and micro-sites with protective nature (e.g. southern sides of fences, debris, wind-protected slopes) for hibernation (Hodek 1993). While we try to simulate this behaviour, the thematic and spatial resolution of the landscape representation naturally restricts our model. Since we can only practically locate some of these micro-sites in the landscape representation, we do not explicitly site them but assume that there are enough micro-sites in landscape patches of the chosen type (e.g., woodland verges).

The mechanisms that regulate the start and the end of hibernation periods in Coccinellidae are notoriously complicated (see Hodek et al. (2012) for review), and the complete account of factors that trigger these behaviours is lengthy, intricate, and still not complete. Moreover, the role of the different factors was reported to be distinct in different locations and populations, even for the same species (e.g., tendencies towards aestivation and multi-volcanism in warmer climates). Taking this into account, our model uses only two factors for which a broad consensus exists among the researchers: the day length and aphid abundance (that could implicitly include temperature and physiological ageing of plants) (Hodek and Čerkasov 1960; Rolley et al. 1974).

C. septempunctata are potentially polyvoltine (Ceryngier et al. 2004). Heterogeneous voltinism appears to be one of the factors responsible for the predominance of *C. septempunctata* in most habitats of the Palaearctic and for its successful invasion of the Nearctic Region (Hodek and Michaud 2008). However, an important limitation of the current model is that it assumes that the ladybird is univoltine. This is a decision taken to simplify the model in its first iteration because, at the latitudes where the use of the model is initially planned, the ladybird is univoltine. However, if the model is used in warmer locations, it will not perform correctly without modification of the voltinism.

Overview of the processes

C. septempunctata is a classic example of a highly specialised forager that preys on particular species of aphids and adjusts its lifecycle accordingly. In a typical case, which represents the life cycle of coccinellids in temperate zones, adults leave the overwintering sites in the spring to feed on wild herbs, shrubs or trees populated with prey early in the season, move between them, then fly to crops

which have been infested early by aphids; they occasionally change between crops where they reproduce. Adults from last year's generation return to tree, shrub, and wild herb hosts before hibernation. Adult ladybirds have a 1:1 sex ratio and emerge from hibernation in mid-spring. If females have sufficient energy, they deposit egg batches from mid-June to early July. They produce, on average, one egg batch every second day (with an inter-oviposition period lasting from 1 to even 6 days). Eggs develop and hatch into larvae with four larval instars before pupation. Adults emerge from the pupae and feed until autumn, when they start to move to hibernacula to overwinter in groups. Emergence is in the spring when aphid populations start to build up, and females lay eggs at locations with aphid prey. Since males are abundant, we make the simplifying assumption that we do not need to model these explicitly after emergence. This life cycle is expressed as a state transition diagram; see Fig. 1.

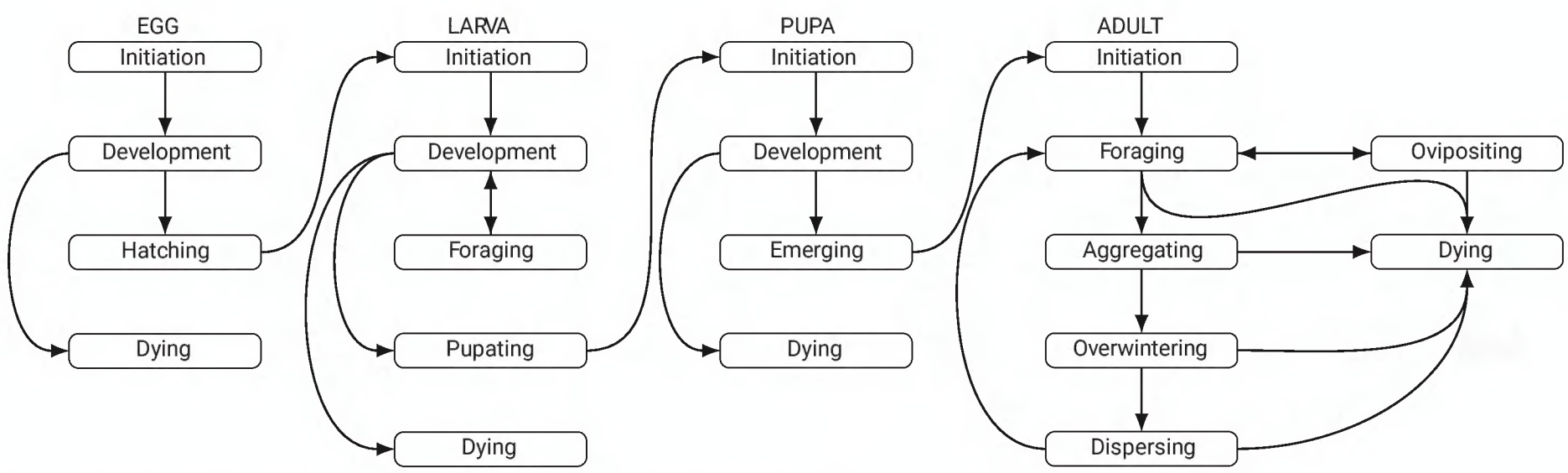

Figure 1. Diagram that depicts the transition between the basic life stages of ladybird.

Juvenile life stages and development

Description

The ladybird is holometabolous (having complete metamorphosis) and passes through the following developmental stages: egg, larva (with four instars), pupa and adult. The total developmental time is around 1–2 months. The egg stage lasts 15–20% of the preimaginal developmental time, the larva 55–65% and the pupa 20–25% (Honěk and Kocourek 1990; Dixon 2000).

Similarly to oviposition, the food quality and quantity affect the ladybird's development time and final size. Hauge et al. (1998) found that *Metopolophium dirhodum* and *Sitobion avenae* were significantly better prey than *Rhopalosiphum padi*, resulting in faster development, likely higher survival and bigger adult ladybirds. *Acyrthosiphon pisum* was significantly better than *Rhopalosiphum maidis* in terms of developmental times and adult weight (Obrycki and Orr 1990). Similar results were found by (Omkar and Srivastava 2003) for developmental weight and size with the same order of species suitability as they found for total oviposition (see Section Oviposition / Prey type). However, when considering development and oviposition scales, it is noteworthy that these two studies (i.e. Hauge et al. 1998; Farooq et al. 2020) disagree on the suitability of *S. avenae* as food compared to *R. padi*. Farooq et al. loc. cit. note, however, that the host plant may affect the palatability and suitability of aphid species to ladybirds, and this has been shown for *Aphis fabae* (Shannag and Obeidat 2008).

If prey quality is constant, then the development and transition between the developmental stages is a function of the temperature and weather (e.g. Ricci et al. 2005). So, depending on the particular year or latitude, the population dynamics pattern could shift over time. A linear model approximates the course of development rate in the ecologically relevant temperature range and enables the calculation of two thermal constants. The first of these is the above-mentioned lower development threshold (LDT), also known as the basal temperature T_b (Trudgill et al. 2005), and this is the temperature below which development ceases. The other constant is the sum of effective temperatures (SET) or, in other words, the thermal time *T*, which is the number of day degrees [*dd*] above LDT for completion of a developmental stage.

Several studies have estimated the fundamental developmental values (LDT and SET) for ladybirds under different conditions (see Obrycki and Orr 1990; Formusoh and Wilde 1993; Omkar and Srivastava 2003; Katsarou et al. 2005), and (Hodek et al. 2012) for an overview of other species. Based on these studies, Skirvin et al. (1997) fitted sigmoid curves to obtain their model's temperature-dependent development rates for the juvenile stages. However, the estimated values do not necessarily concur, and the methods of the studies and treatments differ significantly. There is, however, an agreement on the optimal temperature for development being approximately 30 °C (Xia et al. 1999; Aman et al. 2023). In addition, some studies provide extensive datasets that include the influence of additional factors, such as prey density or prey type, on development (e.g. Xia et al. 1999; Farooq et al. 2020). It seems clear that prey density will change the feeding rate of the larvae and, therefore, their developmental rate. However, the precise effect depends on the prey quality and quantity available.

Assuming constancy of food supply, the daily number of aphids consumed grows with the individual's age, and the relationship is close to linear (Fig. 2).

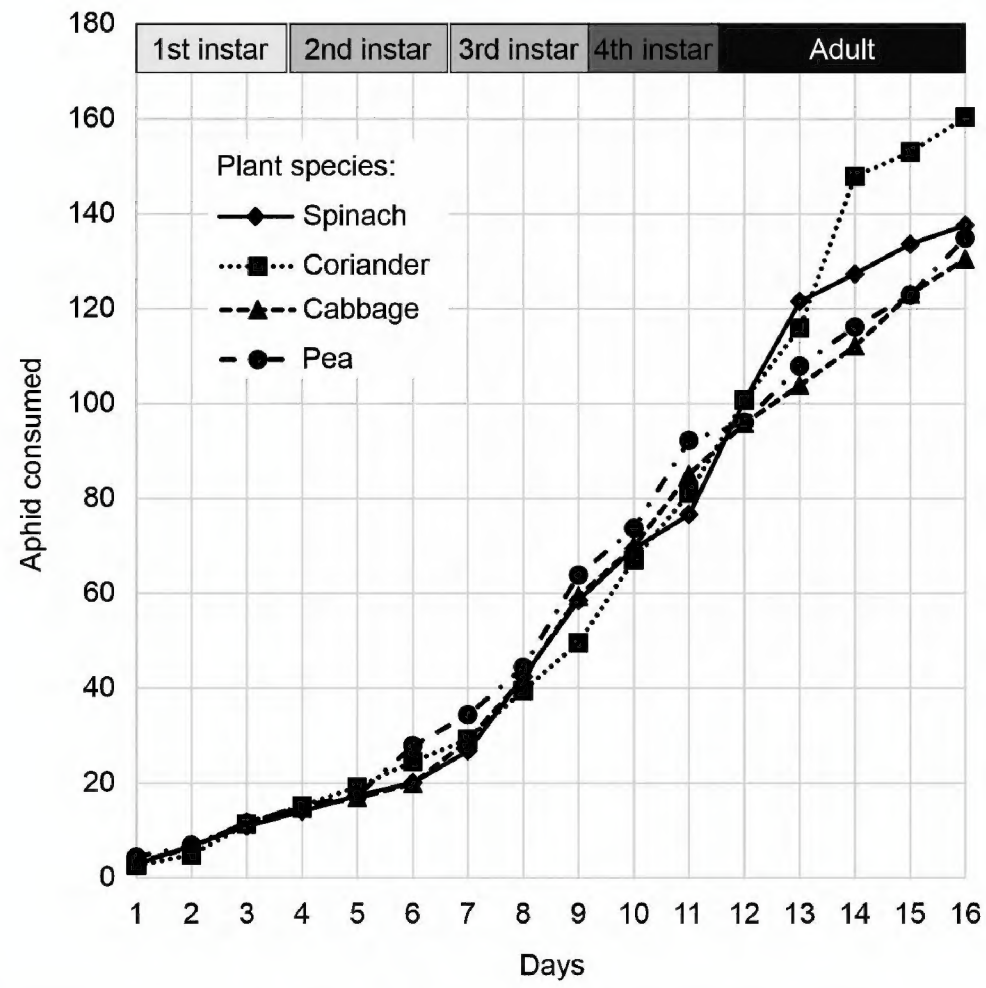

Figure 2. Consumption of different aphid species on four plant species by different stages of *Coccinella septempunctata* in the lab at 25 °C. Pupal stage is ignored. Redrawn from Arshad et al. (2017).

Planned implementation

For the sake of simplicity in implementation, the immobile prepupa stage of the larva is treated as a pupa. In the implementation, we emphasise several important development stages of the juvenile ladybird:

- Eggs to larva (time length T1), which depends on temperature.
- Larva to pupa (time length T2), which depends on temperature but is also affected by the availability of aphid prey.
- Pupa to pre-oviposition imago (time length T3) which depends on temperature.

Hourly air temperatures are utilised to compute the accumulated degree days for each life stage. The developmental constants applied in this calculation are detailed in Table 1, and were estimated to fit the data from Xia et al. (1999).

In addition to temperature, the growth of the larvae is influenced by the density of aphid prey (Table 2). In extreme situations, larvae will die after three consecutive days of starvation. To account for prey quality differences, the prey quality scaler E_A will be applied, as it is for oviposition. This appears to be reasonable since, in almost all cases, growth rates seem to scale with quality of prey. The exception to this rule is that not all studies showed clear differences in larval growth between aphid species, despite these causing differences in fecundity (e.g. Kalushkov and Hodek 2004). However, in this case, all prey species compared were considered to be high-quality food.

For the sake of consistency, we exclusively used the data from Xia et al. (1999) to inform the development equations and parameters. We note that this assumes the prey values are scalable if prey with higher or lower prey quality than the cotton aphid *A. gossypii* is provided using the prey quality scaler E_A. The relationship is linear (the development is faster when the prey level is higher). Practically, this is implemented by the introduction of a prey-level dependence in SET (SET_{prey}; Equation 1).

$$SET_{prey} = SET \times f_L(N_{prey}) \times E_A \quad \text{Equation 1}$$

where the function $f_L(N_{prey})$ factors the SET value, increasing the desirable threshold value when the prey amount is insufficient.

Table 1. Developmental constants used for all juvenile ladybird stages. LDT - lower development threshold; SET – sum of effective temperatures. SET is calculated from the start of each instar and therefore is not cumulative.

Stage	LDT [°C]	SET [dd]
Egg	11.5	42
Larva: instar 1	13.8	22.8
Larva: instar 2	13.6	20.4
Larva: instar 3	13.6	23.1
Larva: instar 4	13.9	38
Pupa	12.9	63.6
Pre-oviposition adults	12.4	151.9

Table 2. Aphid density maximums for calculating prey effects on development rates. Above these values maximum rates are applied. *a*, *b*, *c* are constants from Equation 2 used to calculate the values for Table 1.

Larval instar	Aphids/m^2	*a*	*b*	*c*
1st	45	4.771	-0.1278	0.0014
2nd	45	5.59	-0.1536	0.0019
3rd	80	5.135	-0.0877	0.0006
4th	120	9.5246	-0.0731	0.0003

The values were again estimated from Xia et al. (1999) for each instar. Prey density is assumed to be indexed by the average number of prey eaten per day over the lifespan of the stage. This method increases the length of the stage depending on the food consumed. The levels of prey fed to each instar differed (Xia et al. 1999); hence, the values from the study needed to be translated to relative values of aphids/m^2 for each instar. To do this, a 2nd order polynomial was fitted to the data (Equation 2).

$$f_L(N_{prey}) = \mathrm{a} + \mathrm{b}N_{prey} + \mathrm{c}N_{prey}^{\ 2} \qquad \text{Equation 2}$$

where $f_L(N_{prey})$ is the relative developmental rate compared to the maximum, a, b, and c are constants, and N_{prey} is the number of aphids/m^2 (Table 9).

To implement this in the model, the mean aphid density per day experienced by the larva at each stage is updated daily, and the development time (SET) is scaled daily accordingly. Values above 45 (1st and second instar), 80 (3rd instar) and 120 (4th instar) aphids/m^2 are assumed to be 45, 80 or 120 aphids/m^2, respectively in the calculation of mean aphid densities experienced (Table 3). This fixes maximum development rates to factor 1.0 of the maximum development rate at that temperature.

The lifetime of a female (L_f) in days is calculated after hibernation and is calculated stochastically by the Equation 3.

$$L_f = 4 \times (\mathrm{u}–0.5) \times 10.77 + 147.75 \qquad \text{Equation 3}$$

where u is a random number from a Uniform distribution *U*(*0*,*1*).

L_f would normally not be needed, but would kill the ladybirds if they fail to lay their complement of eggs, e.g. if aphid numbers are too low.

Foraging

Description

Due to ladybirds' role as natural enemies, the relationship between the coccinellids and their prey was one of the first areas of study. Therefore, considerable work has been focused on understanding ladybird prey-searching patterns, prey preference, and the influence of diet on ladybirds' development, reproductive potential, and survival.

Noting that when a toxic aphid, *Aphis sambuci*, was eaten by *C. septempunctata*, having detrimental effects, it was suggested that physiological parameters,

Table 3. The scaling factor for the ladybird larvae development rate at different prey densities. No development assumed at zero aphid densities.

Aphids m^{-2}	1st	2nd	3rd	4th
0	inf	inf	inf	inf
5	2.246	1.959	2.438	1.806
10	1.958	1.707	2.234	1.739
15	1.708	1.494	2.046	1.674
20	1.496	1.319	1.874	1.612
25	1.321	1.182	1.717	1.554
30	1.184	1.083	1.575	1.498
35	1.085	1.022	1.449	1.445
40	1.024	1.000	1.339	1.395
45	1.000	1.000	1.244	1.348
50	1.000	1.000	1.164	1.304
55	1.000	1.000	1.100	1.263
60	1.000	1.000	1.052	1.225
65	1.000	1.000	1.019	1.190
70	1.000	1.000	1.002	1.158
75	1.000	1.000	1.000	1.129
80	1.000	1.000	1.000	1.103
85	1.000	1.000	1.000	1.080
90	1.000	1.000	1.000	1.059
95	1.000	1.000	1.000	1.042
100	1.000	1.000	1.000	1.028
105	1.000	1.000	1.000	1.016
110	1.000	1.000	1.000	1.008
115	1.000	1.000	1.000	1.002
120	1.000	1.000	1.000	1.000
Above 120	1.000	1.000	1.000	1.000

such as growth, reproduction and mortality, should be used as the decisive criterion for diet effects (Hodek 1956). The proposal was to discriminate between two principal kinds of food: essential that ensures oviposition and the completion of larval development, and alternative that serves only as a source of energy and thus prolongs survival in comparison with starvation (Hodek 1962, 1967, 1993). This approach has been widely accepted (Evans et al. 1999; Berkvens et al. 2010). For the list of essential prey in *C. septempunctata* see Table 4.

Studies of different strains of the same coccinellid species indicated important differences in main developmental life history parameters as a function of prey suitability (Michels and Flanders 1992). There is also a significant impact of prey type on mortality (Özder and Sağlam 2003) (Fig. 3).

The diet of the ladybirds can vary with season, depending on prey availability or their stage of development. For example, in early spring (before aphid emergence), *C. septempunctata* feeds on non-aphid arthropods, fungal spores, pollen etc. (Ricci et al. 2005). However, in June and July, its diet consists mainly of aphids. Likewise, the physical size of the ladybird influences the necessary prey density (Yang et al. 2022). The aphid density required by a small ladybird is increased because, due to its size, the ladybird is unable to catch larger aphid instars (in this case, fourth instars and adults); this might be more important with large aphid species (Sloggett 2008).

Table 4. Essential prey of *C. septempunctata*: (G) based on examination of gut content – 'common' food. (L) based on observation of larvae of the coccinellid occurring together with the recorded prey. (O) other source of information (e.g., field observations). Based on different information sources, adapted from Hodek et al. (2012).

Prey type	Source of information
Acyrthosiphon pisum	O
Aphis craccivora	O
Aphis fabae	O
Aphis fabae	L
Aphis glycines	O
Aphis gossypii	O
Aphis gossypii	G
Aphis jacobaeae	L
Aphis nerii (*on Calotropis procera*)	G
Aphis urticata	O
Brevicoryne brassicae	L
Diuraphis noxia	O
Hyalopterus pruni	O
Hyperomyzus lactucae	L
Lipaphis pseudobrassicae	O
Lipaphis pseudobrassicae	G
Longiunguis donacis	O
Macrosiphoniella artemisiae	O
Megoura viciae (*slightly less suitable*)	O
Metopolophium dirhodum	L
Microlophium carnosum	L
Myzus cerasi	O
Myzus persicae	O
Myzus persicae	L
Myzus persicae nicotianae	O
Rhopalosiphum maidis	O
Rhopalosiphum padi	O
Schizaphis graminum	O
Sitobion avenae	L
Sitobion avenae	O
Uroleucon aeneus	O
Uroleucon cirsii	L

Coccinellids spend most of their time searching for prey (Table 5). However, their foraging activities are influenced by several indirect factors, including taxis, plant structure, plant surface, and diurnal periodicity. A decision-making framework proposed by Hodek et al. (2012) suggests that ladybirds navigate through a landscape, landing randomly on plants during foraging. Upon detecting prey, they initiate a localised search pattern, resulting in aggregation in areas with high prey density. Satiation typically ensues, which reduces their tendency to disperse and leads to a localisation of oviposition. Indirect support for this general decision-making framework comes from the observations of aphidophagous coccinellids that oviposit in areas of high prey density (e.g. Dixon 1959; Banks 2009).

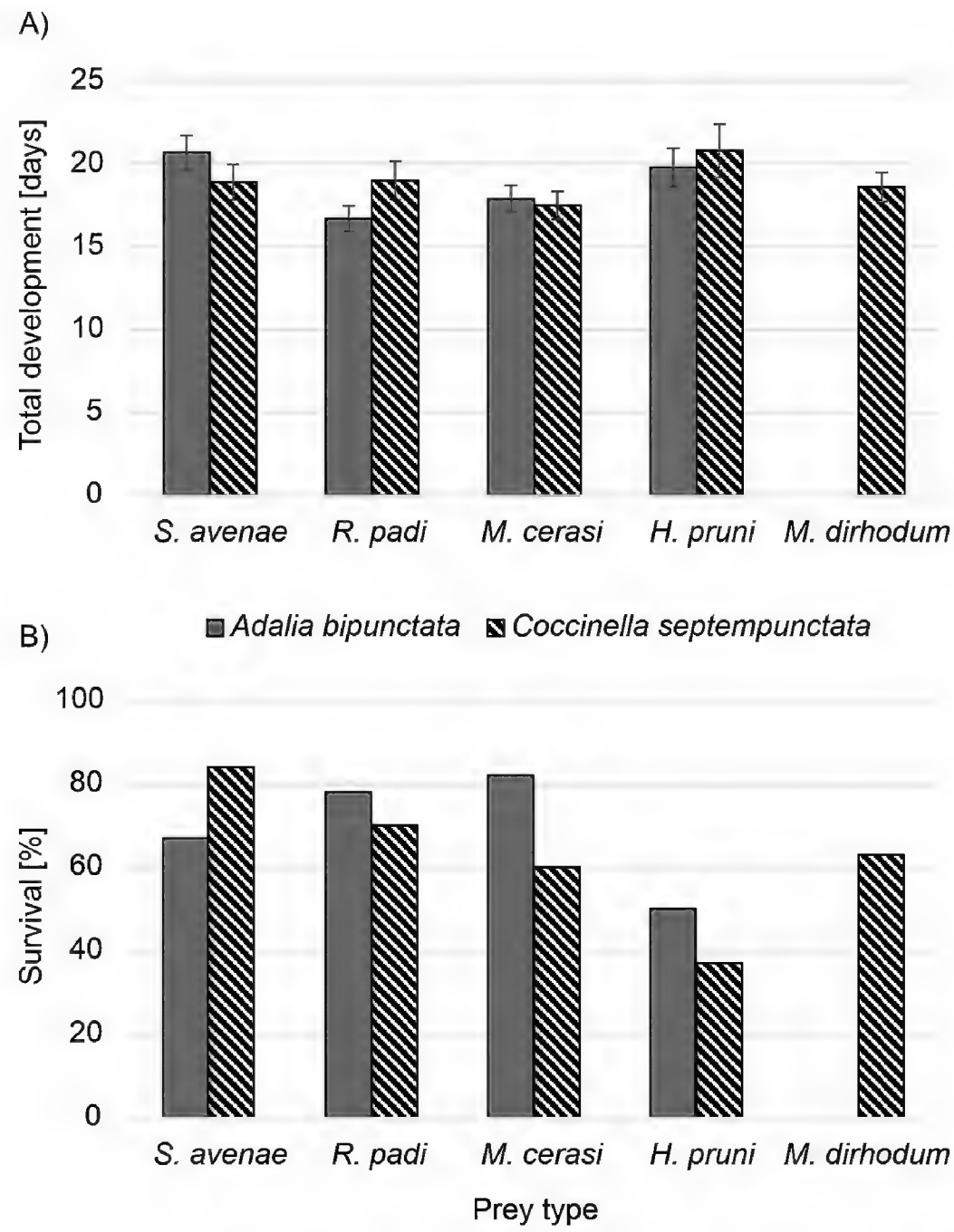

Figure 3. Variation in development and mortality for two ladybirds fed on different prey, based on Özder and Sağlam (2003). *S. avenae - Sitobion avenae*, *R. padi - Rhopalosiphum padi*, *M. cerasi – Myzus cerasi*, *H. pruni - Hyalopterus pruni*, *M. dirhodum - Metopolophium dirhodum*.

Table 5. Time budget (% time) of adult *Coccinella septempunctata* behaviour under experimental conditions (mean + SE) (Minoretti and Weisser 2000).

Behaviour	Aphid-free plant	10 aphid colony	30 aphid colony
Searching	67.0 ± 4.9	63.7 ± 6.8	40.3 ± 6.1
Grooming	4.0 ± 1.7	9.9 ± 3.1	14.6 ± 3.6
Resting	12.3 ± 5.0	8.9 ± 3.9	8.6 ± 4.3
Handling of prey	0	16.9 ± 2.7	24.0 ± 3.4
Feeding on plant tissue	5.4 ± 2.5	1.0 ± 0.8	0.5 ± 0.5
Feeding on nectar	5.4 ± 3.8	2.2 ± 1.3	11.1 ± 4.9

Bianchi and Van Der Werf (2003) described the residence time in a prey patch as being proportional to the aphid density in their searching area (Equation 4).

$$t_r = r_c \cdot \mathrm{A/SAI} \qquad \text{Equation 4}$$

where t_r is the mean residence time (*days*), r_c is the residence time coefficient (*days*/aphids/m^2 search area), which is a scaling factor. *A* is the aphid density (aphids/m^2 ground area), and SAI is the search area index (m^2 of leaf area/m^2 of ground area) of the landscape element.

Literature shows that ladybirds are capable of detecting the substances that can guide them to the prey: honeydew (and sugar in sugar-treated plots; Evans and Swallow (1993)), aphid pheromones, and volatile compounds released by plants attacked by herbivores (Ninkovic et al. 2001). However, the minimum prey density capable of attracting *C. septempunctata* is considered to be ten aphids per m^2 (Honěk 1980).

Planned Implementation

After the dispersal, ladybirds become active and search for food through foraging behaviour. An adult ladybird requires ten aphids daily for sustenance. The nutritional needs of larvae vary across their four instars, with the maximum daily aphid consumption assumed to be 45, 45, 80, and 120 aphids for the first, second, third, and fourth instars, respectively. Larvae are limited to local foraging (see Section Movement / Planned implementation / Short-range movement); should they fail to find sufficient aphids within their allotted daily range, they may resort to cannibalism (Section Cannibalism / Planned implementation). Adults engage in local foraging (Section Movement / Planned implementation / Short-range movement) and long-distance foraging (Section Movement / Planned implementation / Long-range movement) and will commence egg-laying if they encounter an adequate supply of aphids.

Oviposition

The relationship between ladybird fecundity and environmental conditions is the subject of multiple studies. Data has been collected from both the laboratory and field (or semi-field) conditions, and it is challenging to identify a complete set of factors that influence seven-spot ladybird fecundity. However, the age of the individual, the air temperature, the diet composition, and the prey density emerged in the literature review as the most common factors. These are considered below.

Description

Egg batches

Field data shows that ladybird eggs are laid in clutches (batches) on leaves, twigs or other exposed solid substrates. The size of an egg clutch can vary between 6 and 60 eggs. The median clutch size measured in the field is 37.5 eggs (Honek et al. 2008). The median daily oviposition measured in the lab was 38 eggs, the mean daily oviposition was 40.2 eggs, and maximum oviposition rates was 72 eggs per day as observed for ladybirds feeding on *R. padi* (Farooq et al. 2020). *C. septempunctata* preferentially oviposits near the young aphid colonies, often in small clusters in protected sites on leaves and stems. Typically, it is assumed that only one clutch per day is laid (Bianchi and Van Der Werf 2003). However, it is suggested that more than one clutch can be laid per day at low aphid densities, although total egg production at these low densities is lower (Honek et al. 2008). The overall fecundity of the female appears to be fairly constant (Sundby 1968), but also predictably variable depending on temperature and prey density.

Oviposition period

Although the new generation appears around late summer / early fall and mating occurs soon after that, the eggs are laid in spring next year, i.e., after overwintering hibernation and feeding on aphids.

According to Omkar et al. (2004), the oviposition period could be divided into two components: the days when oviposition occurs and the days between oviposition events (i.e., the inter-oviposition periods). The total oviposition period measured by Omkar et al. (2004) was 34.60 ± 1.48 days, of which there were 15.70 ± 2.90 days of oviposition and 18.90 ± 1.66 days of inter-oviposition periods. The inter-oviposition periods spanned 1.93 ± 0.18 days (range 1–6 days) and occurred 10.00 ± 0.59 times (range 6–12 times) in the entire oviposition cycle. The reported total number of eggs laid was 612.10 ± 45.20.

Age of female

Hodek et al. (2012) suggested that the number of ladybird eggs laid per day increases rapidly during several days after adult eclosion, reaching a maximum (which may equate to the number of ovarioles in both ovaries of the female) at approximately two or three weeks. This rate then gradually decreases over the remaining life span of the female, which might be several months. Dixon (2000) suggested that these changes in oviposition rate (a rapid increase followed by a slow decrease) during adult life can be described by a triangular fecundity function. However, the patterns of oviposition with time studied for *Harmonia axyridis*, *Hippodamia variegata* and *Adalia bipunctata* showed a rectangular function with a steep slope to the decline rather than a triangular shape (Lanzoni et al. 2004, Fig. 4). Since we currently do not have sufficient data to parameterise such a model for the seven-spot ladybird, we will assume a simple rectangular function.

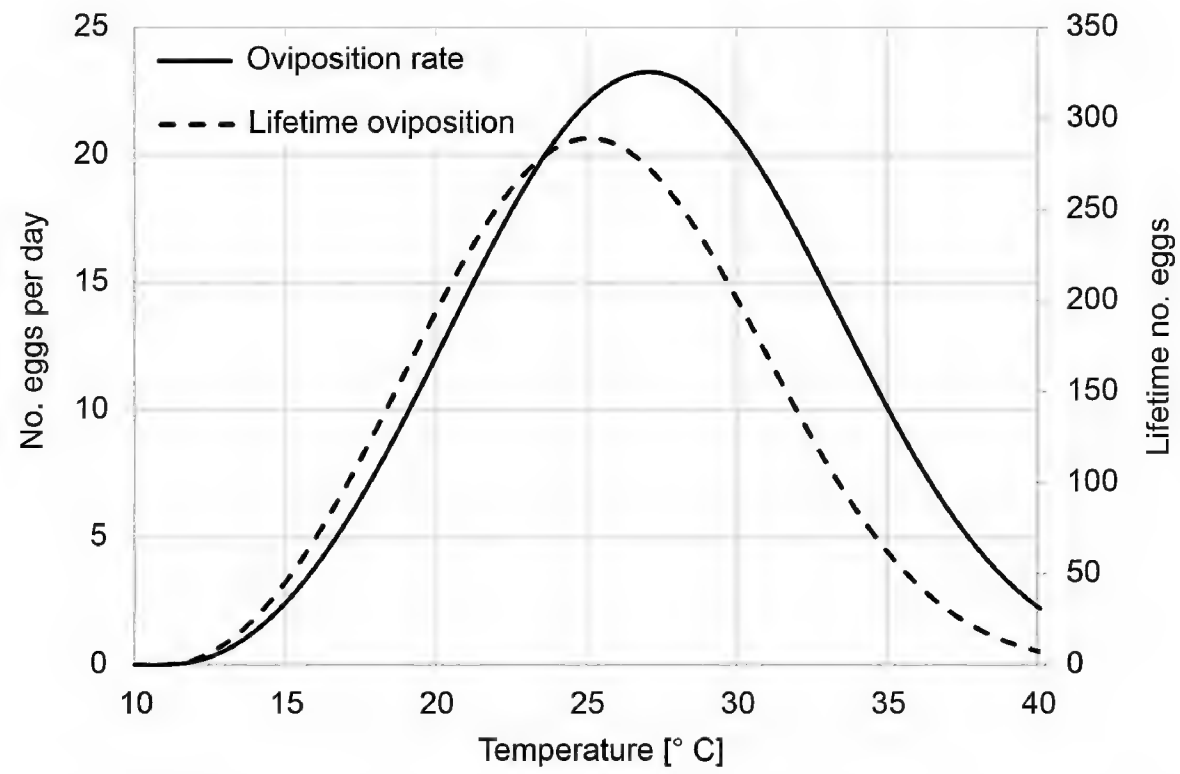

Figure 4. The relationship between temperature and (**A**) lifetime oviposition of the female and (**B**) mean oviposition rate for *Coccinella septempunctata* feeding on the cotton aphid *Aphis gossypii*, calculated using Equation 2 and parameters from Xia et al. (1999).

Prey type

Direct measures of total oviposition come from experiments on *C. septempunctata* feeding on *Aphis craccivora* at 20– 25 °C, 50–70% RH, and 16:8 (L/D) photoperiod. In two pesticide impact experiments, the mean total number of eggs produced was 982 and 1042 (Yu et al. 2014a; Yu et al. 2014b). This corresponds well with a study of Omkar and Srivastava (2003) on the order of suitability of aphid species for *C. septempunctata*, in which egg production of ladybirds feeding on *A. craccivora* was 1060. Studies on the fecundity of *C. septempunctata* indicate that prey type significantly influences fecundity (Table 6). However, there is little consistency in the literature regarding which prey results in what fecundity and evidence of considerable individual variation.

In addition, even when feeding on the same species (*A. fabae*), consumption of aphids reared on a susceptible cultivar increased the female fecundity and fertility by over 30% compared to feeding on aphids reared on a partially a resistant cultivar (Shannag and Obeidat 2008).

Start of oviposition period / End of overwintering

The population settling in the fields and the oviposition start date are driven by the number of aphids. The literature suggests values of aphid density that could be used as thresholds (Table 7). Depending on the crop, different timing and density of aphids may be needed for settling and ovipositing. Once the ladybirds have settled on the field, the ovarioles mature until the second, higher threshold in aphid density is reached, after which the ladybirds start laying eggs. The minimum density recorded for that stage is 334.6 cm^2 of leaf area/aphid (for cereals). The threshold level for oviposition has been assumed to be the same as adult settling (Skirvin et al. 1997). However, as reported by Honěk (1980), levels of aphid density may depend on the crop, although this may be confounded by field-to-field variability due to lack of field replication. Values reported vary from 9.2 to 161 aphids/m^2 with a mean of 73.0 aphids/m^2 (six crops) (Table 7). It was argued that feeding at the correct density of prey trigger the development of ovarioles.

Table 6. Total oviposition of *Coccinella septempunctata* feeding on different types of aphids.

Prey type	Egg production (mean and range, if available)	Reference
Lipaphis erysimi	1764	Omkar and Srivastava (2003)
Acyrthosiphon pisum	1428 (268-2386)	Kalushkov and Hodek (2004)
Sitobion arvenae	1286 (218–2291)	Kalushkov and Hodek (2004)
Myzus persicae	1198	Omkar and Srivastava (2003)
Aphis craccivora	1060	Omkar and Srivastava (2003)
Aphis craccivora	1042	Yu et al. (2014b)
Aphis craccivora	982	Yu et al. (2014a)
Rhopalosiphum padi	787	Farooq et al. (2020)
Aphis gossypii	739	Omkar and Srivastava (2003)
Aphis craccivora	683 (134–1839)	Kalushkov and Hodek (2004)
Aphis fabae	626 (98–1528)	Kalushkov and Hodek (2004)
Schizaphis graminum	553	Farooq et al. (2020)
Uroleucon compositae	488	Omkar and Srivastava (2003)
Sitobion arvenae	370	Farooq et al. (2020)
Rhopalosiphum maidis	360	Farooq et al. (2020)
Aphis nerii	203	Omkar and Srivastava (2003)

Table 7. Density of aphids required for two-phase settling of the population and start of oviposition. Study area was in Caslav (200 m a.s.l.), Praha-Ruzyne (350 m a.s.l.) and Milicin (600 m a.s.l.). After Honěk (1980).

Phase	Crop	Date of observation	Julian calendar date	Mean aphid denisty [aphids/m^2]	Mean leaf area / aphid [cm^2]
Settling of the population (after migration)	Bean	22.05.1978	142	3.7	408
	Sugar beet	24.05.1978	144	3.5	251.2
	Maize	19.06.1978	170	1.2	553.7
	Cereals	22–29.05.1978	142–149	23.6	507.3
	Alfaalfa	19.04–15.05.1978	109–135	7.8	2549.2
	Bean	24–28.05.1979	144–148	0.7	3476
	Cereals	10.05–12.06.1979	130–163	8.7	1789.2
	Alfaalfa	11–17.05.1979	131–137	10.4	3211.3
Start of oviposition	Bean	29.05–06.06.1978	149–157	9.2	260.3
	Sugar beet	30.05.1978	150	19.7	193.6
	Cereals	31.05–2.06.1978	151–153	88.3	334.6
	Alfalfa	1–6.06.1978	152–157	161.3	196.2
	Cereals	11–15.06.1979	162–166	74.5	222.2
	Alfaalfa	24.05.1979	144	84.9	234.8

In Japan, adults that emerged from overwintering appeared in alfalfa fields when daily maximum temperatures exceeded 12 °C, and there was no rainfall (Takahashi 1993). Bianchi et al. (2007) defines the end of overwintering as mid-spring (120 Julian date) and the oviposition period as between mid-June and early July (Julian date 160–190).

Oviposition in relation to temperature

At lower temperatures, female ladybirds do not oviposit. The minimum temperature required for egg-laying is 11 °C (Xia et al. 1999). At 35 °C, the mean oviposition rate is comparable to that at 20 °C; however, the total oviposition per female is much lower. Xia et al. (1999) employed Weibull's model (Weibull 1951) to describe this relationship (Equation 5, Fig. 4).

$$B = \frac{f_2}{f_1} \times f_3 \left[\frac{T - T_1}{f_1}\right]^{(f_2-1)} \times \exp\left(-\left[\frac{T - T_1}{f_1}\right]^{f_2}\right) \quad \text{Equation 5}$$

where B is the oviposition rate or lifetime production of eggs, T is the temperature in °C, T_1 is the threshold temperature of 11.0 °C and f_1, f_2, f_3 are constants (to be calibrated).

We note that there is an unexplained discrepancy of approximately 50% magnitude in the total number of eggs produced in the experiments by Xia et al. (1999) compared to other studies (Omkar and Srivastava 2003; Yu et al. 2014a, 2014b) when comparing maximum overall rates. All studies agree that oviposition was greatest at 25 °C, but Xia et al. (loc. cit.) recorded a mean maximum of 287.4 eggs, compared to 739.2 in the Indian studies.

Daily egg production for *C. septempunctata* reaches maximally 22.4 eggs per female per day (Xia et al. 1999). This daily egg production equates to approximately 42 eggs per batch, assuming inter-oviposition days divided by oviposition days of 18.9/34.6 from Omkar et al. (2004). This range falls within that found by Honek et al. (2008), although it is much below the reported maximum of 72 eggs, which is likely achievable only with high-quality prey.

Oviposition in relation to prey density.

In addition to temperature relationships, Xia et al. (1999) demonstrated a relationship between prey abundance and *C. septempunctata* oviposition rate (Fig. 5). This general relationship is further confirmed by Shahruddin and Ahmadov (2017). This mechanism enables the ladybird to prefer laying eggs in areas with higher prey density, which are more suitable for rearing their brood. The relationship can be described by a negative exponential saturation curve (Equation 6).

$$R_d = c_1 + c_2[1 - exp(-c_3 D_a / c_2)] \quad \text{Equation 6}$$

where c_1, c_2, c_3 are constants (Table 8), D_a denotes the aphid density, and R_d is the oviposition rate or lifetime fecundity.

It is important to note that while this relationship holds generally, it breaks down at local scales, such as individual plants. For example, ladybirds have been observed laying eggs on uninfested plants located near infested ones (Hemptinne et al. 1994).

Planned implementation

The potential oviposition period is regulated by two parameters: the commencement month and the termination month. During this period, the female will attempt to commence oviposition only if it has successfully survived the winter. If these two conditions are met and the female successfully locates a suitable site for egg laying, a day counter will commence. Once the day counter reaches a predetermined value (defined as *Minimum maturation period*), the female will initiate egg-laying.

Table 8. The parameters for Equation 6 provided by Xia et al. (1999).

Parameter	Lifetime No Eggs	Eggs per Day
c_1	-1316.6	-29.2
c_2	1589.9	55.0
c_3	49.04	0.7

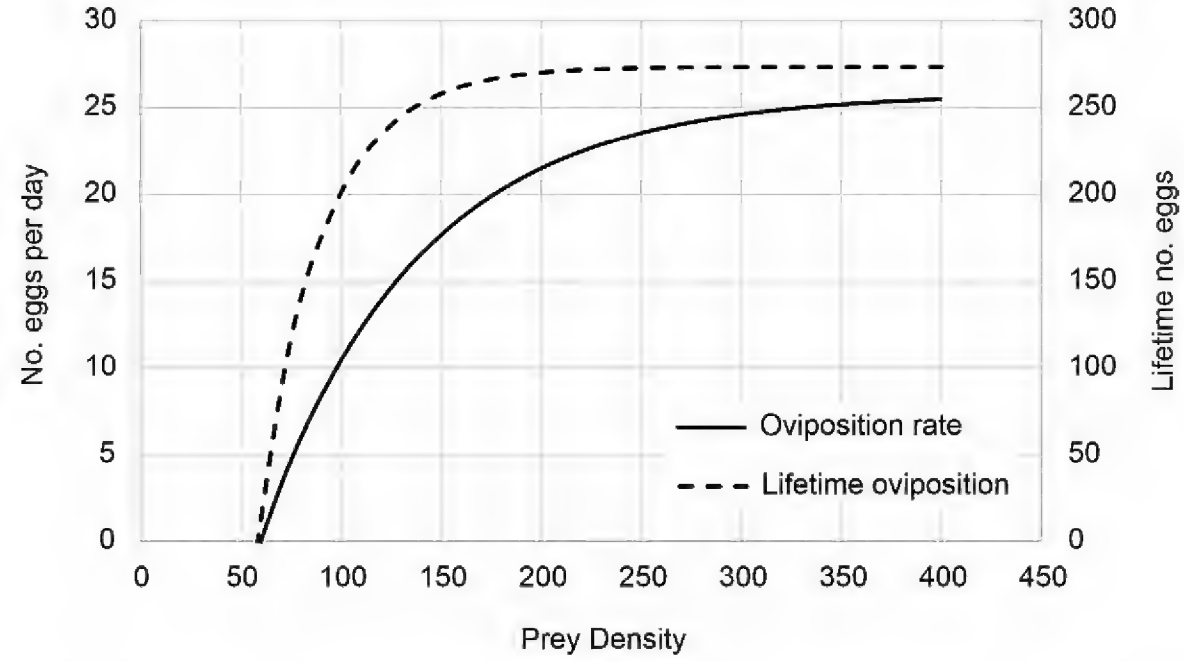

Figure 5. The effect of prey density (number per plant, see Table 9) on lifetime oviposition and eggs per female per day. The experiments were carried out at 25 °C. From Xia et al. (1999) using Equation 6.

Each female can lay a maximum number of eggs in its lifetime. Stochastic variability around this value is added based on what is typical of laboratory studies. The actual lifetime egg number chosen depends on the assumed food quality that the ladybird consumes. Assuming the maximum value reached when feeding on *Lipaphis erysimi* is 1764 eggs, this is 2.3 times the number produced when feeding on *A. gossypii*, according to Omkar and Srivastava (2003). A scaler can then be introduced based on the daily prey consumed (E_A).

Female aphids only lay eggs when the aphid density at a specific location is above predetermined thresholds. This behaviour is influenced by the natural habitats and crops in which they reside, as these environments may have varying thresholds for egg production. Due to a lack of specific information, we assume these thresholds are consistent, but we will include stochastic variation to replicate variation in Table 7. Based on the average temperature from 0 to 50 °C, with a step size of 1 °C, and the prey level, Equation 7 will be used to calculate the daily number of eggs (N_e) to lay.

$$N_e = \lfloor f_T(\lfloor T \rfloor) \times R_d \rfloor \quad \text{Equation 7}$$

where the T represents the daily average temperature in °C, and R_d is the oviposition rate (Equation 6).

$f_T(\lfloor T \rfloor)$ is calculated by Equation 8 and Equation 9 below:

$$g_T(\lfloor T \rfloor) = \frac{\mathrm{f_2}}{\mathrm{f_1}} \times \mathrm{f_3} \times \left[\frac{\lfloor T \rfloor - \mathrm{T}_t}{\mathrm{f_1}}\right]^{(\mathrm{f_2}-1)} \times \exp\left(-\left[\frac{\lfloor T \rfloor - \mathrm{T}_t}{\mathrm{f_1}}\right]^{\mathrm{f_2}}\right) \quad \text{Equation 8}$$

$$f_T(\lfloor T \rfloor) = g_T(\lfloor T \rfloor) \times \frac{\mathrm{C_{max}}}{\max\left(g_T(\lfloor T \rfloor)\right)} \quad \text{Equation 9}$$

where T_t = 11 °C is the temperature threshold below which $f_T(\lfloor T \rfloor)$ = 0, f_1 = 18.22, f_2 = 3.11, and f_3 = 349.5. C_{max} = 45 is the maximum clutch size and max ($g_T(\lfloor T \rfloor)$) is the maximum value from $g_T(\lfloor T \rfloor)$ for the temperature range 12 to 50 °C.

R_d is derived from Equation 6 and parameters for daily egg production from Table 8, multiplied by the aphid scaler E_A to account for prey quality. For simplicity, we assume a refractive period of one day between egg-laying batches. Therefore, every second day, the number of eggs to be laid (N_e) is summed for the previous two days to determine the size of the egg batch to be laid at a certain location. Upon completing its egg-laying cycle, when all eggs are laid and unless already killed, the female is removed from the simulation, representing its death.

The model does not utilise information about the dependence between aphid density and the number of eggs laid by individual ladybirds. However, ladybirds are attracted by the aphids and spend more time in areas with higher aphid density. Consequently, the number of egg clutches is expected to increase in landscapes with high aphid densities, and we expect a linear relationship. This relationship will need to be verified during calibration.

We assume a minimum maturation period of four days before oviposition is possible, based on estimates from literature (Honěk 1980; Lanzoni et al. 2004).

Table 9. Number of young *Aphis gossypii* adults offered daily to individual *C. septempunctata* to determine effect of food supply on bionomics at a constant temperature of 25 °C. From Xia, Van Der Werf, and Rabbinge (1999).

Stage	Level of prey density					
	I	II	III	IV	V	VI
1st	10	15	20	25	30	35
2nd	15	20	25	30	35	40
3rd	20	30	40	50	60	80
4th	40	60	80	100	120	150
Adults	50	80	110	140	170	200

Mortality

Ladybird mortality can occur at any life stage. In this section, we focus on sources of mortality besides parasitism and cannibalism, which are covered in two separate sections below (6.5 and 6.6, respectively).

Description

Stage-dependent survival

The literature studies available provide an account of survival chances for the entire life cycle. Xia et al. (2018) conducted detailed experiments in June 1993, outdoors in field cages with cannibalism included in the mortality (Table 10) and in lab conditions at different temperatures (20 °C, 24 °C, 28 °C). Xia et al. (1999) carried out detailed experiments and modelling on the relationships between mortality and temperature, which are used as the starting point throughout this section.

Temperature-dependent survival

Laboratory measurements at five temperatures for all the developmental stages of *C. septempunctata* clearly show a bi-linear dependence between the mortality and the temperature with an optimal temperature between 25 °C and 30 °C (Xia et al. 1999). The relationship between temperature and relative mortality rate (R_m) was described for all developmental stages as a parabola with three parameters d_1, d_2 and d_3 (Table 11).

Extremely low temperatures during the winter hibernation and freezing and heat waves during the active period can seriously damage the ladybird population. The supercooling point (SCP) is a temperature that causes insects to freeze; the number is generally used to describe cold tolerance in arthropods. The average SCP of fresh eggs of *C. septempunctata* was −27 °C; for older eggs, it was −24.5 °C, probably due to the accumulation of metabolic water in the embryo (Nedved and Windsor 1994). In June and July, wild-collected pupae of *C. septempunctata* had a SCP of 19 °C. At the same time, SCP changes during the season, probably as a function of the outdoor temperature to which the beetles are exposed (Nedved 1993).

Similarly, adults and second instar larvae of a sister species *Harmonia axyridis* were heat stressed at 35 °C, and showed high mortality at 40 °C, but

Table 10. Survival of different developmental stages of *C. septempunctata*. The research was conducted in June 1993 outdoors in field cages. Cannibalism was included in the mortality.

Stage	Survival (%)
Egg	36.8
1st instar	76.0
2nd instar	77.7
3rd instar	75.2
4th instar	74.2
Pupa	74.6
Total survival from egg to adult	9.0

Table 11. Parameters for temperature and relative mortality rate of different life stages of *C. septempunctata* feeding on *Aphid gossypii* on cotton for Equation 10 (below) (Xia et al. 1999). The adult stage was divided into 12 age classes encompassing the maximum ladybird lifespan with three standard deviations added.

Life stage	Age class	d1	d2	d3
Egg		0.3723	-0.03404	0.000817
1st Larval Stage		0.3393	-0.02835	0.000719
2nd Larval Stage		0.097	-0.00792	0.000233
3rd Larval Stage		0.0393	-0.00473	0.000193
4th Larval Stage		0.0107	-0.0012	0.000082
Pupa		0.0959	-0.00914	0.000268
Adult	1	0.034	-0.0028	0.00007
	2	0.116	-0.0091	0.00020
	3	0.094	-0.007	0.00019
	4	0.680	-0.0553	0.00118
	5	0.670	-0.0533	0.00118
	6	1.468	-0.1172	0.00249
	7	1.504	-0.1213	0.00268
	8	1.807	-0.075	0.00132
	9	2.256	-0.1791	0.00392
	10	2.788	-0.2217	0.00484
	11	3.836	-0.3095	0.00672
	12	5.358	-0.4202	0.00887

all other stages tolerated these hot conditions (Acar et al. 2004). In experiments with *H. axyridis*, 100% mortality occurred in the egg and pupal stages at 35 °C (Hodek et al. 2012). The supercooling point (-17 °C) and lower lethal temperature (-16.7 °C) remained relatively constant for the overwintering populations in the outdoor hibernaculum. Similar patterns to those of *C. septempunctata* have been observed in this species, with SCP declining in winter (Watanabe 2002).

Survival in relation to the prey density

The lab observations also provide insight into the dependence between the prey density and the chances of larval survival. Larval survival decreases with decreased larval density (Bista and Omkar 2014) and cannibalism increases with decreased larval density (Sato et al. 2009). The study by Xia et al. (1999) provides a comprehensive data set which forms a solid basis for developing a relationship for implementing the model (Fig. 6).

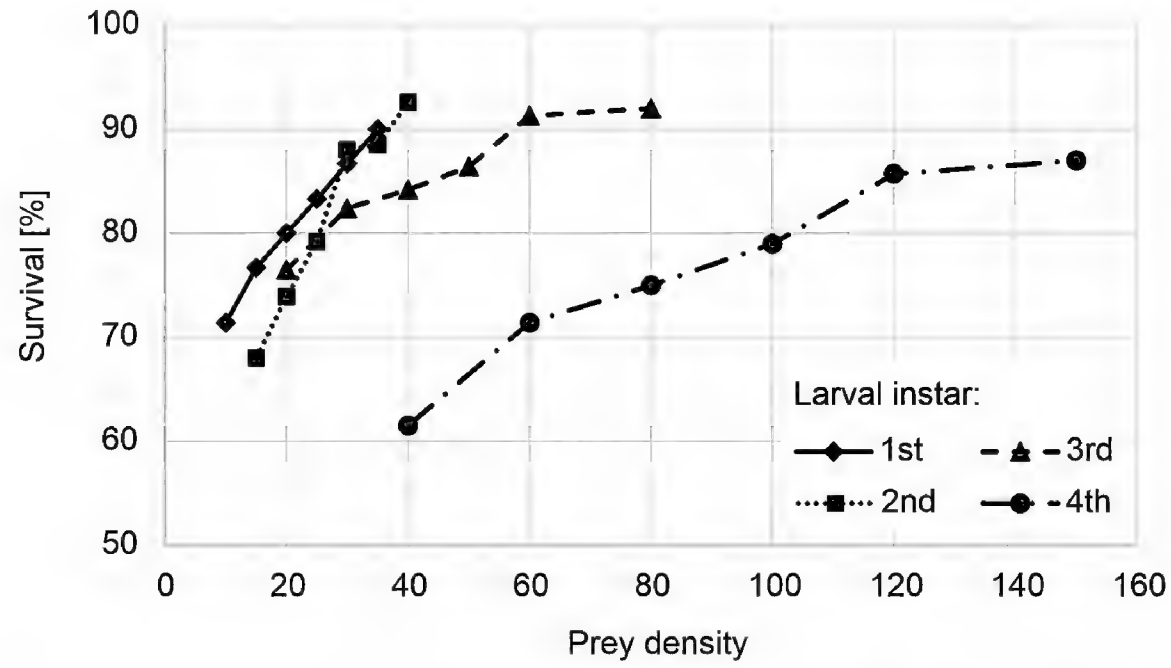

Figure 6. Larval instar survivorship at different prey densities (Xia et al. 1999). Prey density – number of young *Aphis gossypii* adults offered daily to individual larvae of *C. septempunctata*.

Overwintering mortality

Ceryngier (2015) report that multiple authors emphasise the importance of energy reserves (fat, glycogen) in determining ladybird survival during dormancy. Experiments and observations show that the overwintering survival of *C. septempunctata* is positively correlated with their weight relative to body size measured at the beginning of overwintering (Zhou et al. 1995; Barron and Wilson 1998). As the differences in the 'relative weights' are clearly dependent on the size of their fat reserves, this is good indirect evidence for a relationship between fat reserves and winter mortality in *C. septempunctata* (Ceryngier 2015).

As noted, the ladybirds form hibernacula, and the size of these also affects winter mortality. A study from the Czech Republic found that the average winter survival rate was 48.4%, with a range of 0% to 88.7% between hibernaculae. No impact of gender was recorded and body size had an inconsistent effect (Honek 1997). Honek et al. (2007) note that the clumped distribution and its effects on winter survival are not properly understood, and that though untested, aggregation has been interpreted as a protection against predators and/or parasitoids, and that "by contrast, easy spread of disease is probably the most important disadvantage of clumping and the potential advantage of clumping must be greater than its risk". In fact, infection with pathogens may occur during dormancy due to the presence of pathogenic spores at the dormancy sites (Ceryngier 2015).

Planned implementation

Different types of mortality will be implemented depending on the source of the mortality.

Farming

Farming activities, such as intensive soil processing, can be connected to increased mortality. The list of activities that have non-zero mortality chance is provided in Table 12. Note that in ALMaSS, pesticide applications are often treated in detail, and the implementation of this will be considered in the application of the model on a case-by-case basis.

Table 12. Agricultural activities that have non-zero mortality in ladybirds.

Activity	Egg mortality	Larva mortality	Pupa mortality	Adult mortality
Harrowing	0.5	0.5	0.5	0.27
Ploughing	0.5	0.5	0.5	0.27
Using Stubble Cultivator	0.5	0.5	0.5	0.27
Autumn roll	0.5	0.5	0.5	0.27
Autumn sowing	0.5	0.5	0.5	0.27
Insecticide application	0.0	0.8	0.8	0.8
Bed forming	0.5	0.5	0.5	0.27
Bulb harvesting	0.5	0.5	0.5	0.27
Harvest	0	0	0	0.25
Mechanical Weeding	0	0	0	0.29

Temperature

The temperature-related mortality implemented in our ladybird model used values derived from Xia et al. (1999). They provided parameters for a 2nd order polynomial for the relationship between relative mortality and temperature for each life stage (Table 11; Fig. 7). Equation 10 is used to generate the temperature-based mortality (M_T) rates at 5 °C intervals of the temperature (T) for inclusion in the model.

$$M_T = d_1 + d_2 T + d_2 T^2 \qquad \text{Equation 10}$$

Parameters d_1, d_2 and d_3 provided by Xia et al. (1999) (Table 11) for the adult stage depend on adult's age, expresssed in the form of 12 age classes. These 12 age classes encompass the maximum ladybird lifespan with three standard deviations added. Unfortunately, there is no clear statement about what maximum lifespan was used. It is also notable that provided adult lifespans are short, suggesting that diapause phase was not considered by Xia et al. (1999). Thus, to be able to use parameters from Xia et al. (1999) in Equation 10, the value for ladybird maximum ladybird must be assumed.

Farooq et al. (2020) recorded prey-type dependent mean lifespans of up to almost 60 days. This is in the middle of the range recorded by Omkar and Srivastava (2003) (44–85 days, dependent on sex and prey species). In contrast, Kalushkov and Hodek (2004) recorded a mean female longevity of 68–78 days on four different aphid species. Hence, initially, we will assume 72 days, this being easily divisible by 12; meaning that each age class from Table 11 spans six days. However, no additional penalty for low prey was applied to allow them to survive without aphid populations early in the year (see Section Foraging).

Hibernation mortality

It will depend on the size and temperature extremes of the hibernacula clump. If the clump size is smaller than 3, the mortality chance is 0.14, while it is 0.07 when the clump size is not smaller than 3 (see details in Section Diapause and Hibernation / Planned implementation). These mortality chances are applied once at emergence. These values are lower than the mean of 48% from the literature because they are subsequently combined with parasitoid mortality and extremely low-temperature mortality to give the correct total mortality and range after the calibration.

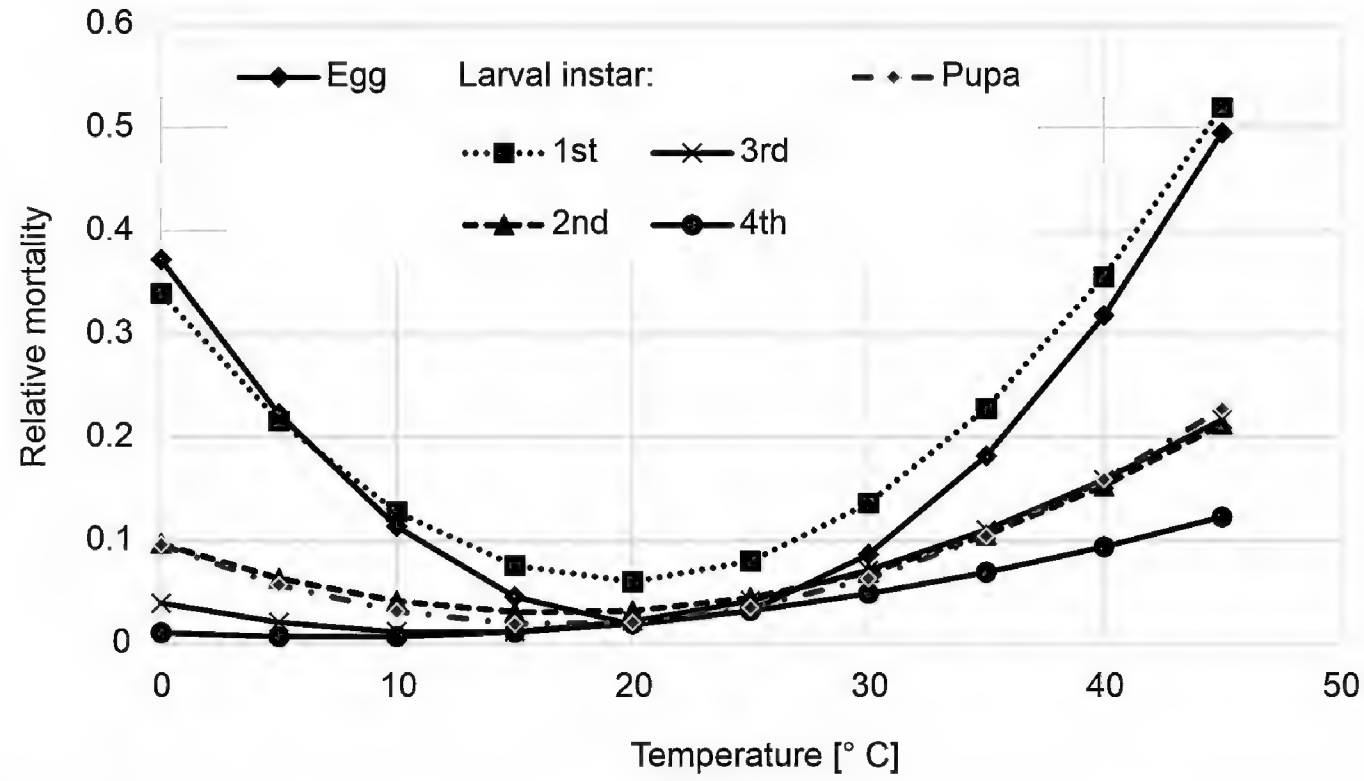

Figure 7. Relative mortality with temperature for non-adult life stages re-calculated from Xia et al. (1999).

To implement extremes of temperature, an extra mortality of 25% is applied during hibernation as a single mortality chance if extremes have occurred (Table 13). For this, the SCP is used as a minimum mortality threshold. SCP ($t_{extreme,min}$) is different for each month of the year and corresponds to (Nedved 1993), January to December: -15, -15, -10, -9, -5, -5, -5, -5, -5, -9, -12, -17 °C. Because ladybirds hibernate in groups and hide in insulated places, the dormant ladybirds are assumed to have effectively lower SCP (by 20%, calibrated value), if in a hibernaculum with more than five ladybirds. A maximum extreme mortality threshold is $t_{extreme,max}$ = 40 °C for all the stages (including adult). This mortality is currently assumed to be in addition to the standard hibernation mortality, but this assumption may need to be evaluated during calibration. For non-hibernating ladybirds of all stages, extreme temperature mortality is assumed to be applied daily when the extremes occur.

Other mortalities

To account for all other mortalities, an individual's mortality is regulated by random variables drawn at each step of the simulation. Each stage will be assumed to have a specific daily chance of mortality, which will be a fitting parameter. Parasitoid and cannibalism mortalities are considered in their separate sections below.

Table 13. Miscellaneous parameters related to mortality. See Table 11 for parameters based on Xia et al. (1999), and Table 12 for parameters related with farming activities.

Parameter name (including the symbol)	Value	Units	Parameter type	Source
Extreme temperature mortality chance	0.25	–	Assumed	
Hibernation bonus (in SCP)	0.2	–	Assumed	
Min temperature for non adult stages $t_{extreme,min}$	-20	°C	Estimated based on literature	Nedved and Windsor (1994)
Max temperature for non adult stages $t_{extreme,max}$	45	°C	Assumed	

Parasitism

Description

Parasitism is an important factor that affects mortality and reproduction chances in coccinellids. Beetles are more vulnerable to a parasite while dormant. Main parasite that affects *C. septempunctata* is *Dinocampus coccinellae* (Schrank). *D. coccinellae* is a braconid wasp attacking adult ladybirds, primarily females (Cartwright et al. 1982), although this is not always consistent (e.g. Koyama and Majerus 2008). The parasitoids oviposit during late summer, but the eggs rest in the body cavity until the following spring and only develop when the host leaves the hibernating site and starts to feed (Ceryngier 2000). It seems that olfactory cues can contribute to the orientation of the wasp towards its prey (Pettersson et al. 2005). The ladybirds usually survive the parasites' emergence but are weakened and usually die within a few days.

Parasitism rates in *C. septempunctata* have been recorded as high as 33% post-dormancy (Triltsch 1996; Ceryngier 2000), but may be very variable during the season (0 to 33%) (Triltsch 1996; Kızıltepe et al. 2009; Soleimani and Madadi 2015). Lipa et al. (1975) recorded 20% mortality by parasitoids and diseases including microsporidian species of *Nosema coccinellae*, *Gregarina coccinellae* and *Gregarina ruskowski* (fungi), and parasitoid *Perilitus coccinellae* (synonom *Dinocampus coccinellae*). Koyama and Majerus (2008) found 12.2% +/- 1.8% parasitisation by *D. coccinellae* in field-collected populations of ladybirds. Ceryngier (2000) showed that the parasitisation rate may differ depending on the location of the hibernation site. In Poland, the parasitisation rates of populations hibernating at the mountain tops (> 1.300 m a.s.l) were much lower (15 to 25%) than of those hibernating at the lower altitudes (800 m a.s.l.; > 70%).

Planned Implementation

In the model's early version, parasitism dynamics are simplified. The effect of parasitism is included as an extra one-time stochastic mortality when the adults disperse from hibernacula. We assume an initial value between 0 and 33% with a central tendency. The parasitism mortality (M_p) is sampled from the uniform distribution (Equation 11).

$$M_p \sim U(0,0.33) \quad \text{Equation 11}$$

Cannibalism

Description

Intra-guild predation and cannibalism by or on predatory coccinellids is very common, and the seven-spot ladybird is a characteristic species in that sense (Dixon 2000; Lucas 2013). These behaviours are influenced by several factors, including prey aggregation (Dixon 1987), richness and abundance of competitors (Rosen 1990), drastic changes in body size (almost five-fold during the immature life stages), and mobility of ladybirds during the life cycle. There is a relationship between the intensity of cannibalism and the abundance of

prey (aphids). Thus, cannibalism is more common when aphid prey is scarce and decreases when the prey becomes abundant (Şengonca and Frings 1985; Agarwala and Dixon 1992; Lucas et al. 1998; Sato et al. 2009). At the same time, if the amount of aphid prey increases, the chance of intra-guild predation increases, probably due to predator competition (Nóia et al. 2008). The outcome of cannibalistic interactions is size-dependent; eggs and young larvae are more vulnerable to cannibalism than older larvae. Literature states that adult coccinellids are never successfully attacked (Hodek et al. 2012).

Four hypotheses were built to describe the reason for cannibalism in general and cannibalism of the ladybirds in particular (Lucas 2013):

I. The predator attacks its intra-guild prey to protect itself before a period of high vulnerability;
II. The predator eliminates a competitor;
III. Through the act of cannibalism, the predator satisfies its nutritional needs. Therefore, cannibalism occurs during extra-guild food shortages or when alternative food is scarce;
IV. The predator selects the prey according to its size, regardless of its guild.

Sibling egg cannibalism in ladybirds has been shown to minimise starvation risks prior to dispersal (Khan and Yoldaş 2018). Therefore, the coccinellid eggs often hatch synchronously, typically within 10 minutes, to avoid being eaten by siblings. Michaud and Grant (2004) investigated three aphidophagous Coccinellidae species that lay clustered eggs, *Cycloneda sanguinea*, *Harmonia axyridis*, and *Olla v-nigrum*, and found that 50–60% of eggs hatched synchronously, while 20–40% were cannibalised by siblings, depending on the species. Early-hatching larvae can consume the remaining eggs. When the larvae cannibalise conspecific eggs, they will develop faster, have lower mortality, and the duration of the first moult will be shorter (Pervez et al. 2022).

Table 14 summarises various laboratory studies on the cannibalistic behaviour of *C. septempunctata*. However, in these studies, the chances of cannibalisation events may have been overestimated. For example, Takahashi (1987) showed cannibalism increasing with the larval stage in mass-rearing experiments, which do not represent natural conditions. Therefore, the extent to which we can infer natural cannibalism from laboratory studies is hard to determine.

There is also potential for sexual dimorphism in regard to cannibalistic behaviour. Males of *Adalia bipunctata* consumed an average of 35.2 out of 40 eggs offered (88%), whereas females consumed significantly fewer, averaging 23.2 out of 40 eggs (58%, Table 14) (Agarwala and Dixon 1992).

Planned Implementation

Since we currently only consider one species, intra-guild predation is ignored. We adopted hypothesis III in the model, implementing cannibalism as a 'last resort' for a ladybird. Cannibalism occurs only when a ladybird cannot locate any aphids to consume, prompting it to cannibalize younger individuals. Regardless of the success of a cannibalisation attempt, the adult or larva subsequently moves in search of areas with higher aphid density. Each stage can only eat the less advanced stage: instar four can only eat instars one to three and eggs, instar three

Table 14. Fraction of the ladybirds cannibalised in different studies.

Presence/ absence of aphids	Stage of the attacker	Proportion of the Ladybird stages eaten in 24 h							Species studied	References
		Egg	1st instar	2nd instar	3rd instar	4th instar	Pupa	Adult		
Aphids absent	1st instar	0,67	0,67	0	0	0	0	0	*Coccinella septempunctata*	Şengonca and Frings (1985)
	2nd instar	1	0,67	0,83	0	0	0	0		
	3rd instar	1	0,83	1	0,83	0	0	0		
	4th instar	0,5	0,67	1	0,83	0,5	0	0		
	Adult	0,5	1	1	0,83	0,67	0	0		
Aphids present	1st instar	0,17	0	0	0	0	0	0	*Coccinella septempunctata*	Şengonca and Frings (1985)
	2nd instar	0,33	0	0	0	0	0	0		
	3rd instar	1	1	0	0	0	0	0		
	4th instar	0,67	1	0	0	0	0	0		
	Adult	1	0,5	0,67	0,33	0,5	0	0		
Aphids absent	1st instar	0,24	0,1	NA	NA	NA	NA	NA	*Adalia bipunctata*	Agarwala and Dixon (1992)
	2nd instar	0,44	0,28	0,15	NA	NA	NA	NA		
	3rd instar	0,72	0,51	0,51	0,2	NA	NA	NA		
	4th instar	0,88	0,6	0,55	0,31	0,3	NA	NA		
	Adult male	0,88	0,82	NA	NA	NA	NA	NA	*Adalia bipunctata*	Agarwala and Dixon (1992)
	Adult female	0,58	0,83	NA	NA	NA	NA	NA		
Aphids absent	1st instar	0,27	NA	NA	NA	NA	NA	NA	*Coccinella septempunctata*	Khan and Yoldaş (2018)
	2nd instar	0,39	0,26	NA	NA	NA	NA	NA		
	3rd instar	0,74	0,77	0,84	NA	NA	NA	NA		
	4th instar	0,86	0,86	0,85	NA	NA	NA	NA		
	Adult male	0,53	0,77	0,75	NA	NA	NA	NA		
	Adult female	0,95	0,88	0,9	NA	NA	NA	NA		
Aphids present	1st instar	0,12	NA	NA	NA	NA	NA	NA	*Coccinella septempunctata*	Khan and Yoldaş (2018)
	2nd instar	0,17	0,01	NA	NA	NA	NA	NA		
	3rd instar	0,23	0,03	0,03	NA	NA	NA	NA		
	4th instar	0,26	0,05	0,07	NA	NA	NA	NA		
	Adult male	0,19	0,03	0,03	NA	NA	NA	NA		
	Adult female	0,33	0,05	0,06	NA	NA	NA	NA		

can only eat instars one to two and eggs, and so on. Cannibalism is only implemented for larval stages; adult cannibalism is ignored in the current model.

Nutritional demands drive cannibalistic behaviour in this model, necessitating the tracking of ladybird appetite to determine daily behaviour. Cannibalised individuals are assigned a nutritional value, which is assumed to be consistent within each life stage or larval instar. The nutritional value was estimated from the comparison between the mean weight of the ladybird stage and an aphid, see Table 15, based on Honek, Dixon, and Martinkova (2008) and calibrated values of sister species from the study of Sengonca and Arnold (2003).

Diapause and hibernation

Diapause is a complex behaviour that allows individuals to alter or completely stall some of the biophysical processes in their bodies. In ladybirds, the adaptive functions of diapause are (i) to synchronise the development of active stages with favourable conditions and (ii) to enhance the survival potential during unfavourable periods (Hodek et al. 2012). Such periods could be prolonged periods of sub-zero temperatures and overly hot and dry seasons that can occur in summers (aestivation diapause).

Table 15. Sizes and assumed nutritional values (in aphids) of different life stages of *Coccinella septempunctata*, estimated from Honek et al. (2008) and Sengonca and Arnold (2003). * not edible.

Life stage	Nutritional value (in aphids)	Weight [mg]
Egg	1	0.2
Larva, instar 1	10	2
Larva, instar 2	30	3
Larva, instar 3	80	8
Larva, instar 4	120	12
Pupa*	140	14
Adult*	160	16

Diapause in ladybirds has been an active field of research for decades (Hodek et al. 2012). Primarily it was viewed as an adaptation for surviving sub-zero temperatures, with a focus on hibernation diapause induced by shorter days and lower temperatures. Later, aestivation diapause was recognised, where the inducing environmental cues are long day length and high temperature. While hibernation diapause can be completed spontaneously without any change of conditions, aestivation diapause is often terminated by a decrease in day length and temperature (Masaki 1980).

Description

Since the first studies (Dobrzhanskii 1922), experimental research has indicated a very wide plasticity in *C. septempunctata* (Obrycki and Tauber 1981; Phoofolo and Obrycki 2000; Hodek and Michaud 2008), enabling heterogeneous activity in different fractions of populations. This is especially true regarding the multivoltine vs. univoltine behaviour, which can differ even within various regions of Europe (see Hodek et al. (2012) for a thorough review). Generally, while populations inhabiting Northern and Central Europe are predominantly univoltine, the alternations in temperature, food abundance or length of day (experimental) can potentially trigger multivoltine behaviour (Jöhnssen 1930; Hämäläinen and Markkula 1972). However, naturally, the second generation is extremely rare in colder climates, with ladybirds mostly dying in the egg or larva phases. At the same time, the southern populations, such as those in southern-eastern France (Iperti 1966), exhibit partial multivoltinism (Bodenheimer 1943), and some isolated observations from southern Spain (Hodek and Okuda 1993) report bivoltine behaviour. Hagen (1962) described six patterns of voltinism for European coccinellids, ranging from single generation with hibernation to multiple generations with or without aestivation. *C. septempunctata* appears to possess sufficient plasticity to exhibit several of these patterns.

However, in cold and temperate climates like Central Europa, *C. septempunctata* spends 2/3 of its lifespan in hibernation. The adults stay at the diapause sites from July/August to April/May (which corresponds to the maximum flying activity in April and August; Boiteau et al. (1999)). However, the exact times are subject to geographical factors. Ladybirds normally choose to hibernate at lowland sites with warm microclimates (southern slopes and woodland margins, roadside), under dead leaves or various debris, in dry vegetation, singly or in

small groups. Not all individuals hibernate, some stay active looking for food (Tauber et al. 1986). At the same time, the overwintering mortality in the hibernating ladybirds is recorded to be significantly lower than in the active ones (Barron and Wilson 1998; Carrillo et al. 2004; Koch et al. 2004).

It has been stated that for diapause, *C. septempunctata* often looks for prominent landscape features, e.g., peaks or large rocks. After gathering around a potential hibernation place and spending some time there (Hodek et al. 1993; Hodek et al. 2012), ladybirds use possibly olfactory stimuli as a cue (Al Abassi et al. 1998) to find other individuals already present at the hibernacula (Hagen 1962; Hodek and Honêk 2013). *C. septempunctata* can overwinter up to 2000 m altitude in Europe (Ricci et al. 2005). However, observations of large aggregations in rocks on mountains have been questioned because of the potential misidentification of the specimens (Hodek and Honêk 2013).

Aggregation is probably a protective strategy against predators and/or parasitoids. Adults can form clumps on substrates such as rock debris and grass (Honek et al. 2007; Hodek et al. 2012). The seven-spot ladybirds form small to medium-sized clumps (relative to other coccinellids) even if the adults are abundant (Honek et al. 2007), with clump size varying with population density (Fig. 8). Ladybirds tend to use the same hibernaculae in the same landscape year after year. The information transfer mechanism is not exactly known, but it could be via olfactory cues (Al Abassi et al. 1998) or thanks to individuals that survive to the second hibernation.

The literature identifies several factors that trigger diapause in ladybirds (Hodek and Čerkasov 1961). The change in photoperiod is considered the dominant factor, with temperature playing a considerable modifying role. Long day lengths have been shown to retard diapause (Obrycki et al. 2024). In addition, there are reports, albeit from other species, indicating that the physiological ageing of plants and consequent changes in aphid populations can influence diapause (Rolley, Hodek, and Iperti 1974).

Overwintering typically ends around April (around 110–120 day of year; Bianchi et al. (2007)). While some authors refer to a photoperiodic trigger to the emergence (Hodek et al. 1977), others state that no specific diapause-ter-

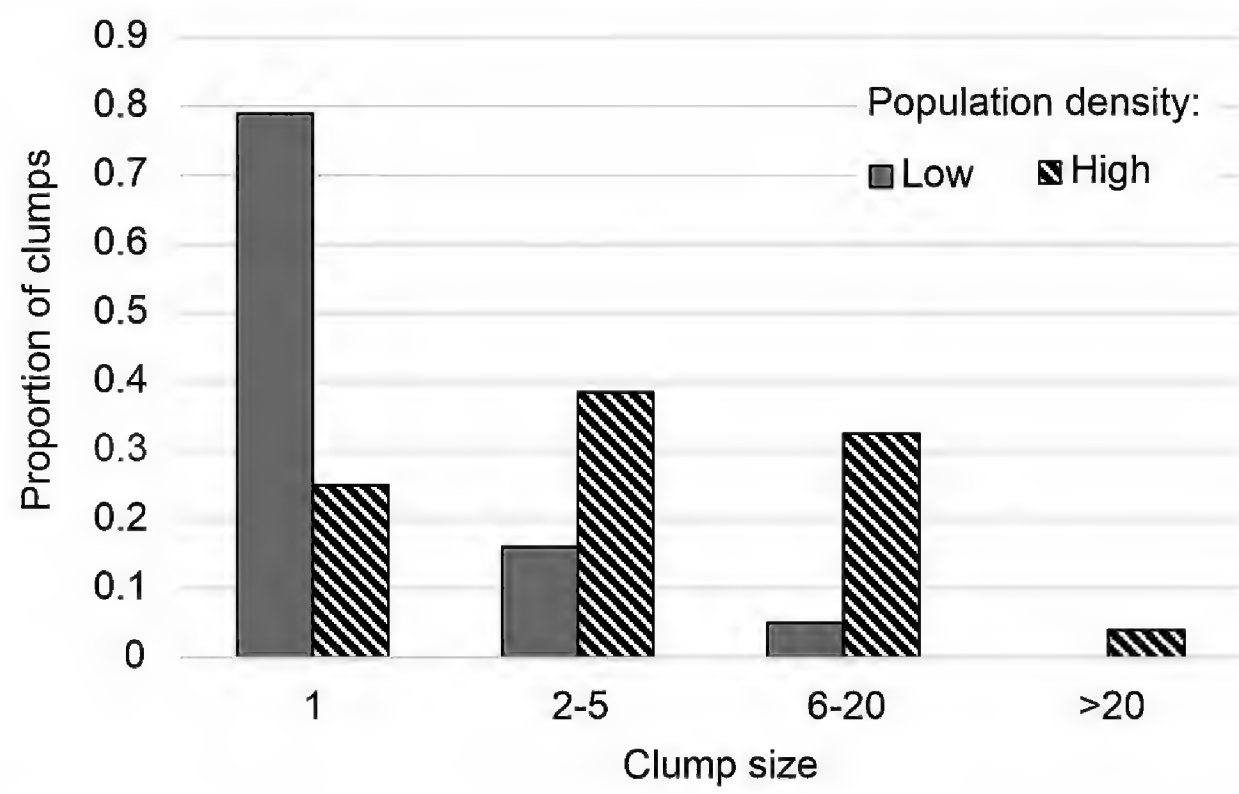

Figure 8. Distribution of clump sizes from low and high density populations of *Coccinella septempunctata* after (Honek et al. 2007).

minating stimulus has been identified (Tauber et al. 1986). Usually, overwintering ends before the emergence of aphids; thus, the first prey of *C. septempunctata* is necessarily different.

Planned Implementation

In this model, only the overwintering diapause is implemented, excluding aestivation diapause. Aestivation is disregarded due to its rarity in Northern and Western Europe, where we intend to apply the model.

The landscape features that ladybirds are looking for in the search for hibernation places are types of landscape connected with rocks or forest/orchard edges. Currently, we ignore the possible tendency of ladybirds to prefer southern slopes and mountainous areas.

The primary triggers for hibernation are photoperiod (explicit through the first and last aggregation day) and decrease in temperature and physiological ageing of the plants (implicitly through the aphid density). The ladybirds cannot stay active after the last day of aggregation. Ladybirds will initiate aggregation under the following conditions (Table 16):

From August to December, when the day length falls below a set value, d_F:

- If the aphid density drops below $N_{aphids,low}$ diapause behaviour is triggered.
- There is a p_{hib} chance of beginning aggregation when aphid density ranges from $N_{aphids,low}$ to $N_{aphids,high}$.

After a ladybird finds a suitable location for hibernating, it will do nothing but wait until the beginning of next year. At the beginning of next year, the clump size will be calculated in a 100 × 100 m^2 rectangle centring on the ladybird's location. There are three categories based on the ladybird density in this local surrounding: category (1) with less than 10 ladybirds, category (2) with ≥ 10 of ladybirds but < 100 ladybirds, and category (3) with 100 or more ladybirds. Subsequently, the hibernation clump size will be determined using probabilities outlined in Table 17, which categorizes clump sizes into four distinct groups. Two smaller clump-size categories will result in a mortality rate of M_{Hs} during hibernation, while the mortality rate for the two larger clump-size categories will be M_{Hl} (Table 16). Aggregation movement is described in the movement section (Section Movement / Planned implementation / Long-range movement), and we assume that the target habitats are linear features such as forest edges, road verges or hedgerows.

The photoperiod also drives the end of overwintering. The aggregation will cease when the day length exceeds d_L minutes. The ladybird will have a 10% chance to wake up from hibernation when the day length is longer than t_E minutes if it passes the mortality test based on the clump size (see section Mortality / Planned implementation), and can switch to movement behaviour if the temperature allows (see section Movement / Planned implementation / Long-range movement).

Movement

During larval and adult stages of their development, ladybirds engage in movement. Eggs and pupa do not move. While the larvae can only walk, the adults combine walking with flying. Adult ladybirds often do not remain long in any

Table 16. State variables for aggregation and hibernation. Berlin is taken as a central point in Europe, but this could be used as a variable and will be subject to the calibration of phenology.

Parameter name (including the symbol)	Value	Units	Parameter type	Note
The last day of aggregation d_L	750	Minutes	Assumed	Day length in Berlin on day 263
The first day of aggregation day length d_F	685	Minutes	Assumed	Day length in Berlin on day 293
Day length t_E at emergence day d_E	755	minutes	Estimated from literature	
Daily chance of emerging after emergence day d_E	0.1	–		Less than one to stagger emergence
Aphid density threshold $N_{aphids,high}$ restraining hibernation after d_F:	1000			
Aphid density threshold $N_{aphids,low}$ triggering immediate hibernation after d_F	10	Aphids number in m^2	Assumed / Calibrated	
Chance to hibernate when aphid density $N_{aphids,high} > N_{aphids} > N_{aphids,low}$ (p_{hib})	0.1	–	Assumed / Calibrated	
Maximum number of beetles in hibernacula $N_{beetles,max}$	20	–	Estimated from literature	
Mortality rate for smaller clump size M_{Hs}	0.14	–	Estimated from literature	
Mortality rate for larger clump size M_{Hl}	0.07	–	Estimated from literature	

Table 17. The cumulative proportion of ladybirds distributed per clump size at three densities. Estimated from Honek et al. (2007). Density is relative, expressed as ladybirds per tussock which we implement as per square meter.

Ladybird Density	Clump Size			
	1	2–5	6–20	20 - $N_{beetles,max}$
Low (<10)	0.77	0.95	1.0	1.0
Medium (10–99)	0.51	0.80	0.975	1.0
High (100+)	0.25	0.65	0.95	1.0

given location but appear to move frequently between sites and habitats throughout the breeding season (Ferran and Dixon 2013). We have divided the movement behaviour into long- and short-range movements.

Ladybird populations are sustained by habitats with aphid presence during the breeding season, as documented in the literature (e.g. Bianchi et al. 2007; Honek et al. 2008). These descriptions, however, are not definitive; the presence of aphids is considered the critical factor. For instance, Skirvin et al. (1997) assumed that immigration of adult coccinellids into the modelled field requires a minimum threshold aphid density of 10 aphids/m^2, based on the findings of Adams (1984) and Honěk (1980).

Description

Short range movement

For both larvae and adults, the average distances that the individuals cover during daily foraging linearly depend on the number of aphids. Ladybirds engage in intensive prey searches through walking and short-range flying. This localised dispersal resulting from switching between habitats to maintain the

ladybird population (Hodek et al. 2012) can create a cyclic colonisation pattern in agroecosystems. This pattern is also affected by the spatial configuration of crop and non-crop habitats (Burgio et al. 2006). Indeed for this reason complex landscapes have a greater potential for providing biological control (Raymond et al. 2015).

While adults can both fly or walk, larvae lack wings and are restricted to walking. Adult walking speed is linearly dependent on temperature, with a minimum temperature threshold of 4 °C (Frazer and Gilbert 1976). The study by Elliott et al. (2000) yielded similar values for three other ladybird species. The larvae are generally assumed to remain within a 20 × 20 m^2 area where their egg has hatched (Bianchi et al. 2007). Larvae combine two types of movement behaviours: extensive search characterised by rapid and straight bursts (runs) and intensive searching behaviour characterised by sinuous trajectories and slow movement with many stops (Ferran and Dixon 2013).

Long range movement

The ladybirds fly to move to distant locations, possibly many kilometres away. This behaviour is common before and after hibernation (i.e., to and from hibernacula, around May and July accordingly) (Hagen 1962). In addition, at times of low food abundance, coccinellids sometimes perform prolonged flights, usually searching for new foraging sites.

Adult coccinellids use vision to locate a perspective patch of vegetation or find prey within a patch (Nakamuta 1984; Obata 1986; Harmon et al. 1998). While ladybirds do not fly during the night, just after sunrise, beetles warm up, exploring the insects in close proximity and waiting for air temperature to become warm enough to engage in flying activity (Van der Werf et al. 2000). Studies indicate the conditions when the flight is possible: minimum required temperature is 15 °C, and the wind speed should not exceed 20 m/s (Sarospataki and Marko 1995). The most intensive flight activity is observed at temperatures higher than 22 °C, and wind speeds lower than 10 m/s.

The dispersal flight at the end of the hibernation was described by Hodek et al. (1993) as a step-wise process. The coccinellids disperse from the hibernacula to look for aphids, and when the aphids are present, they only gradually disperse further. Although the rate of ladybird diversity in alfalfa patches was not correlated with aphid abundance, aphid density correlated well with seven-spot ladybird density (Cardinale et al. 2006). Similarly, earlier studies point to a specific threshold in aphid density that influences a decision to stay at a particular point and start foraging (Honěk 1980). The densities of aphids required for settling differ for different crops and have been expressed as leaf area/aphid (see Table 7).

When there are not enough aphids in the vicinity of an adult ladybird, the coccinellids tend to fly away (Evans 2003), thereby switching to an 'extensive search' mode that coincides with a wider search radius. Once the patch with a higher aphid density is located, the small-scale intensive search behaviour is triggered (Bianchi et al. 2007; Table 18). Ladybirds switch back to extensive search if no further prey is available (Ferran and Dixon 2013). Supporting this behaviour, Frazer and Gilbert (1976) observed no recapture of *Coccinella californica* in alfalfa fields when aphid densities dropped below a certain threshold.

Table 18. Parameters that describe the dispersal of seven-spot ladybird (Bianchi et al. 2007). *d* (in days) stands for the mean residence time.

Parameter	Value	Unit
Residence coefficient	0.002	$d(aphids(m^2 \text{ leaf area})^{-1})^{-1}$
Threshold for switching to extensive search	100	Aphids $(m^2 \text{ ground area})^{-1}$
Radius of dispersal for extensive search (for truncated uniform distribution)	100	m
Radius of dispersal for intensive search (std of normal distribution)	60	m

During long flights, ladybirds can be carried to high altitudes on thermal currents and subsequently disperse on winds at these heights (Hodek and Michaud 2008). Occasionally, this phenomenon can occur across a large area simultaneously, which results in large groups of dispersing coccinellids being passively carried together by wind currents. These currents then deposit the beetles all in the same place in the landscape (Hodek and Michaud 2008).

Diapause and migration events are determined in the late larval or post-adult-emergence stage. At this point, the ladybird may feed voraciously, and it is assumed that the accumulation of sufficient reserves triggers the onset of diapause (Hodek et al. 2012). The flights towards the aggregation sites are directional, and the adults choose landscape landmarks and olfactory signals to direct themselves. As noted in section above, studies show that the day length is a typical signal for initiating aggregation behaviour (Hodek et al. 2012). The aggregation points can be local or remote (e.g., in the mountains). Individuals migrating to remote hibernation sites are typically larger and enter diapause earlier in the season. Others stay in lowland areas, making shorter flights to the hibernacula in nearby suitable habitats. Some ladybirds remain at the breeding areas and will diapause in the shrubs, margins, or hedgerows around forest edges (Hodek 1993).

Planned Implementation

There are two movement types planned for implementation: short-range movement (walking or short flights, considered as walking) and long-range movement (flying). Short-range movement simulates intensive search behaviour when the adult ladybird or larva scans the local surroundings in search of prey. It is performed in steps until either a maximum movement distance is reached or a suitable density of aphids is found. Here, Equation 13 (see below) is applied to calculate maximum movement distance. Long-range movement simulates the extensive search for a different type of landscape element or vegetation. This movement could be either part of aggregation or dispersal behaviour or a response to insufficient resources at the current location. Details for the implementation of both types of movement behaviours are presented below, with state variables provided in Table 19.

Short-range movement

In the model, short-range movement can occur one meter at a time in any of the eight possible directions, until the maximum daily movement distance is reached. Larvae and adults have distinct maximum movement distances.

Table 19. Movement-related state variables in the *Coccinella septempunctata* model.

Parameter name	Value	Units	Parameter type	Reference
Maximum number of movement steps *Mn*	15	–	Assumed	A trade-off between searching efficiency and computing power.
Maximum flying distance $L_{flying,max}$	500	m	Estimated from literature	Maes et al. (2014)
Searching (proportion of daylight hours for movement)	0.71		Assumed based on the literature	Minoretti and Weisser (2000)
Minimum short-distance movement SM_T	4 (larvae) 12 (adults)	m	Assumed	Based on Bianchi and van der Werf (2004) for larvae. For adults to move them out of the current aphid patch.
Temperature-dependent speed of short-range movement (only if temperature > 10 °C)	0.0325	m/min/° C	Calculated above	
Minimum temperature threshold for long-range movement	15	°C	Estimated from literature	Sarospataki and Marko (1995)
Maximum wind speed threshold for long-range movement	10	m/s	Estimated from literature	Sarospataki and Marko (1995)
Minimum temperature threshold for short-range movement	4	°C	Estimated from literature	Frazer and Gilbert (1976)
Aphid density threshold for ladybird settling A_t	10	Aphids/m^2	Estimated from literature	Honěk (1980); Skirvin et al. (1997)

Larvae move less than adults, but at least four meters per day, to fit with Bianchi et al. (2007). The adults move at least 12 meters per day (SM_T). For adults walking, the dependence between the daily distances covered and the temperature is implemented through the maximum daily time budget (see Table 5). We assume that, for approximately 71% of the daily active time, the ladybird searches for prey. Then, time *t* for movement can be calculated as (Equation 12):

$$t = 0.71 \times daylight_time \quad \text{Equation 12}$$

where $daylight_time$ is the sunrise to sunset measured in minutes.

If we assume that *C. septempunctata* walking speed linearly increases with temperature, and that this dependence can be described as a mean of regression lines estimated for three species of ladybirds (*C. maculata*, *H. tredecimpunctata and H. convergens*) by Elliott et al. (2000), the temperature-dependent speed of movement is (1.00–0.35)/(34–14) = 0.0325 m/min/degree. Thus, the maximum short movement distance (S^A_d) for adults is calculated based on the average air temperature (T_A) and day length (D_L) when T_A > 10 °C using Equation 13 presented below.

$$S^A_d = 0.71 \times D_L \times 0.0325 \times T_A \quad \text{Equation 13}$$

For larvae, the maximum daily movement distance S^L_d equals $S^A_d/2$.

For 4 °C < *T* < 10 °C, we assume that the distance covered by an adult ladybird is two m per day to allow some minor movement, while for larvae, it is one m per day (i.e. half the adult movement). Equation 13 yields very high movement rates at higher temperatures, e.g., 200 m at 20 °C; thus, this will need to be considered in the model calibration. However, it is important to realise that these movements are convoluted and do not represent a net distance travelled from a point.

The direction of short-range movement is decided upon out of eight cardinal directions with a even probability of 0.125. An individual will choose one direction first and move $SM_T/2$ for larvae and SM_T individual steps for adults along that direction, assess the habitat for settling, and if the aphid density is too low, choose another random direction for the next movement. This sequence will continue until either settling conditions are met or S_d^A distance is reached. For larvae, aphid density above zero will stop movement.

Long-range movement

Long-range movement requires a minimum temperature of 15 °C, and wind speed not exceeding 10 m/s (24 hr mean). Two types of long-range movement are possible, either related with foraging behaviour (triggered when aphid densities are low or after hibernation) or with movement towards hibernation sites. In both cases, a target condition is provided (aphid density or habitat type).

We assume that the ladybird has a minimum flight distance $L_{flying,max}$. Starting in a random direction, the ladybird spirals out from this location until it finds a suitable location or uses all its movement allowance. The movement allowance is given by $Mn * L_{flying,max}$.

This method has been selected based on the experiences of other models to represent an animal searching efficiently from a point location. Thus, long-distance movement can be used to move rather short distances, and this will implemented in the case of local aphid depletion when the same method will be used, but the initial movement will be SM_T. This method will need to be carefully calibrated after model implementation.

Discussion

Our approach to the ladybird model is highly detailed compared to previous attempts at ladybird modelling, enabled by the dynamic and realistic landscape simulation provided in ALMaSS. This detailed approach in an agent-based modelling framework will allow the emergence of population patterns based on a mechanistic combination of processes. These emergent patterns will also include the results of local feedback interactions, which can give rise to interesting non-linear dynamics and provide a basis for improved prediction (Topping et al. 2015).

This level of detail offers another advantage: it allows for a high degree of flexibility for the subsequent calibration, as the emergent patterns represent different hierarchical levels, from individual traits to population processes. However, as noted in the 'Framing the Model' section, not all processes could be included. We reduce some potentially important processes to simple stochastic probability functions due to a lack of knowledge, which limits the model's behaviour.

In developing the mechanisms and parameters suggested for the first version of the model, we encountered several difficulties. One is that literature studies rarely provide enough context when presenting the resulting data. Features such as weather, location, and surrounding habitats are often missing from the description of methods. Some experiments also have issues with low numbers of individuals, leading to uncertainty around the parameter values (e.g. Sengonca and Arnold 2003). Generally, a lack of information is a problem when developing such detailed models.

A similar problem leading to parameter uncertainty relates to the laboratory data used. Laboratory data is the primary source of information for the model and is typically a set of experiments where parameters are altered one by one. For example, Xia et al. (1999) looked at the effect of temperature or aphid numbers on development times and fertility. However, in the natural world, parameters co-vary and are not constant. Thus, when we develop our parameters from this type of data, we assume that several factors contribute to the output, but the combinations still need to be tested. The choice of how we combine the parameters is, in effect, a hidden parameter. For example, see Equation 4 and Equation 7, which could be expanded and include more parameters to alter the shape of the responses to aphid density.

Fixed temperatures from laboratory experiments result in another difficulty for the model, which must operate in a variable environment. The problem relates to modelling the relationship between temperature and development. We use a simple day-degree model because there is insufficient data to parameterise the more realistic biophysical model (Wagner et al. 1984), or even more complex thermal performance curves (Angilletta 2006). The biophysical model better represents development at the upper and lower range of possible development thresholds and thus will perform better when extremes of temperature occur. The thermal performance models provide a more accurate representation of fluctuating temperature effects and a more realistic response to high temperatures. However, these models require more information than is available at present. An additional uncertainty is that translating laboratory temperature to field temperature across various micro-climatic sites means that laboratory and field development rarely give a one-to-one correlation. Thus, we expect that calibration will result in an adjustment of many of these parameters.

Due to limited knowledge and the need for tractability, we also had to restrict the factors influencing behaviour. For instance, the factors that limit the population size will have a crucial influence on the model. Here, we decided that the number of hibernacula is not a limiting factor in the model; therefore, ladybirds can always find a hibernation site within the landscape modelled. We based this decision on a literature description of different possibilities for siting hibernaculae: “In lowlands the usual dormancy sites of *C. septempunctata* are situated at forest edges, in clearings or in windbreaks. If no such site is close by, *C. septempunctata* hibernates near isolated shrubs or other plants, or on slight unevenness of the terrain” (Hodek and Honêk 2013). It is difficult to imagine a landscape without an abundance of these locations, but this might be an issue in very intensive agricultural landscapes. This issue may be resolved by incorporating a density relationship to parasitism; however, it is not currently implemented.

Another factor requiring expert knowledge was related to reproduction. We assume that there is no limiting factor in finding mates. Ladybirds mate often, changing partners (Banks 2009; Hodek et al. 2012). Therefore, a potential decrease in the number of males (e.g. due to parasitism) would have a minimal effect on the population, primarily due to a reduced positive effect of polyandry (Haddrill et al. 2007). Therefore, to increase the model’s efficiency, we do not simulate males. Similar approaches are used in other ALMaSS models (Bilde and Topping 2004; Ziółkowska et al. 2023).

While we follow literature data and mechanisms as faithfully as possible, there are some situations where heuristic algorithms cannot be avoided. The best example is movement. These algorithms are built based on our understanding of how the mechanics of decision-making work for the agents in our model, given the level of information available in the in silico environment. Consequently, artefacts in model output may occur due to these less realistic mechanisms. This issue is unavoidable but should be considered in the next developmental step, i.e. calibration and testing.

Overall, the ladybird model should strike a good balance between detail, the data needed to support the detail, and the practicality of implementing and eventually applying the model. As noted in the limitations section, many aspects could be included if either data or functional details in ALMaSS were available. Nevertheless, the seven-spot ladybird serves as a representative species within the Coccinellidae family. This makes the model broadly adaptable to other ladybird species, provided that sufficient species-specific data can be obtained.

ALMaSS is designed to evaluate management strategies and their impact on indicator species. As such the ladybird model presented here could be evaluated with regard to its response to the improvement of habitats and the recently observed impacts on this species (Magagnoli et al. 2024). Studies which show corellations of the response of *C. septempunctata* and other aphid predators could then be used to evaluate the extent to which the ALMaSS ladybird model might represent the aphid predator guild, and to what extent other ladybird models need to be developed.

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Conflict of interest

The authors have declared that no competing interests exist.

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Use of AI

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Data availability

All of the data that support the findings of this study are available in the main text.

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